

# Five New Cenozoic Epitoniids from Southern Peru and the Neogene History of *Scalina* Conrad, 1865 (Gastropoda: Epitoniidae) in the Americas

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**Abstract.** Five new fossil species of the epitoniid genus, *Scalina* Conrad, 1865, are reported from the Pisco Basin of southern Peru: *S. foosei*, sp. nov. (late Eocene), *S. brophyi*, sp. nov. (early Miocene), *S. belti*, sp. nov. (early Miocene), *S. isaacsoni*, sp. nov. (middle Miocene), and *S. cheneyi*, sp. nov. (late Miocene to early Pliocene). *Scalina ferminiana* (Dall, 1908) is formally reported for the first time from upper Pliocene beds of northern Peru. During the Paleogene, American species of *Scalina* ranged from the northeastern Pacific Ocean to southern Peru and throughout the Gulf of Mexico. Neogene American taxa from warm subtropical and tropical waters with uncertain Paleogene ancestry are assigned to one of three groups arising from within a 'brophyi' clade: an 'isaacsoni' clade of sharply reticulate taxa extending from the middle Miocene to Recent that presently inhabit the eastern Pacific Ocean and both western and eastern Atlantic Ocean, a 'pseudoderoyi' clade of broad-spined species with anteriorly ramped spiral cords that arose during the late Miocene and persists today in the eastern Pacific and western Atlantic Oceans, and a 'brunneopicta' clade of narrow-spined populations with numerous spiral cords that also arose during the late Miocene and exists today only in the eastern Pacific Ocean. The most significant American Tethyan radiation of *Scalina* took place well before the closure of the Isthmus of Panama.

## INTRODUCTION

Epitoniid gastropods of the genus *Scalina* Conrad, 1865, can be distinguished from cancellate species of *Amacea* H. Adams & A. Adams, 1853, by their contrasting basal and lateral spiral sculpture. Five Recent species of *Scalina* have been described from the eastern Pacific Ocean (Weil et al., 1999). *Scalina ferminiana* (Dall, 1908) ranges from Mexico to northern Peru (Dall, 1908a; Alamo & Valdivieso, 1997). The other four species are found only on the Mexican or Central American coast [*S. brunneopicta* (Dall, 1908), see Dall (1908a), *S. tehuacanarum* (DuShane & McLean, 1968)], only in the Galapagos [*S. pompholyx* (Dall, 1890)], or from Mexico to the Galapagos [*S. deroyae* (DuShane, 1970)]. Two species of *Scalina* are recognized in the western Atlantic Ocean: *S. mitchelli* (Dall, 1896) and *S. retifera* (Dall, 1889). The latter species also occurs in the eastern Atlantic Ocean (Ardovini & Cossignani, 2004).

Several Neogene species of *Scalina* have been described from the eastern Pacific and western Atlantic Oceans, including taxa from Maryland (Martin, 1904), Jamaica (Guppy, 1874; Woodring, 1928), Venezuela (Jung, 1965), Panama (Olsson, 1942; Woodring, 1959), Mexico

(Böse, in Böse & Toula, 1910; DuShane, 1977), California (Keen, 1943; Addicott, 1970), Ecuador (Pilsbry & Olsson, 1941; DuShane, 1988), and northern Peru (DeVries, 1986). No fossils of *Scalina* had been reported from southern Peru, nor have any yet been described from Chile (e.g., Philippi, 1887; Tavera, 1979; Nielsen et al., 2004). Paleogene species of *Scalina* are widespread in North America, with species ranging from Alaska, possibly (Durham, 1937), and Washington State (Durham, 1937; Weaver, 1942) to the southeastern United States (MacNeil & Dockery, 1984); none had been reported from western South America.

This paper documents late Pliocene occurrences of *Scalina ferminiana* in northern Peru, the first Miocene and Pliocene examples of *Scalina* from southern Peru, the first Eocene species of *Scalina* from western South America, and addresses the late Cenozoic evolutionary history of *Scalina* in the Americas.

## GEOLOGY

The stratigraphy of the Cenozoic Pisco Basin in southern Peru (Figure 1) has been described by Muizon & DeVries (1985), Dunbar et al. (1990), DeVries & Schrader (1997), DeVries (1998, 2004), and DeVries et al. (2006). Within this forearc basin, the middle to upper Eocene Paracas Formation overlies crystalline bedrock. Unconformably overlying the Paracas de-

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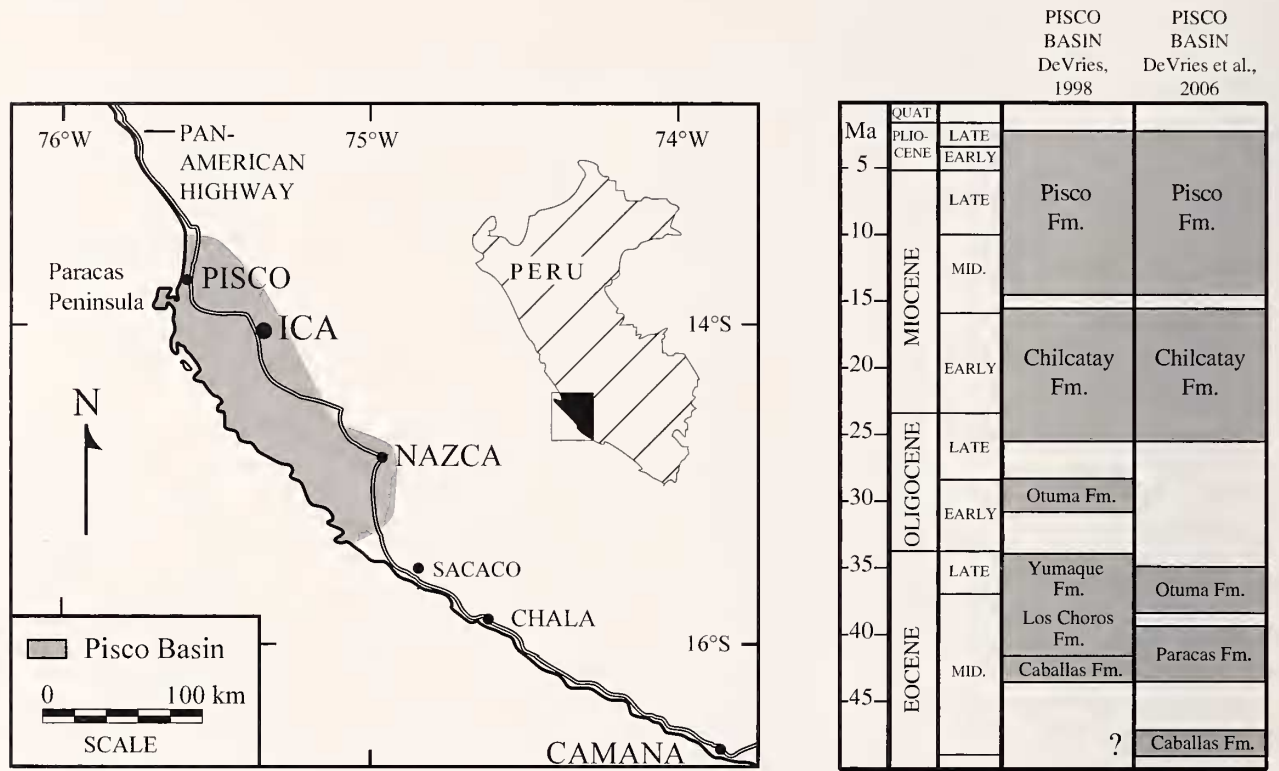


Figure 1. Locality and Cenozoic stratigraphy of the Pisco Basin in southern Peru. Specimens of *Scalina* occur in the Otuma, Chilcatay, and Pisco Formations.

positional sequence is the uppermost Eocene Otuma Formation, which in turn is overlain by the uppermost Oligocene to middle Miocene Chilcatay Formation and middle Miocene to Pliocene Pisco Formation. Each Cenozoic formation is characterized by a transgressive sandstone member representing nearshore paleoenvironments and a finer-grained, tuffaceous, and diatomaceous silty sandstone member representing outer shelf paleoenvironments. Fossils of *Scalina* are usually found in the nearshore sandstones.

METHODS AND MATERIALS

All Peruvian fossils in this study were found by the author. Geochronologic ages are reported by Muizon & DeVries (1985), Dunbar et al. (1990), DeVries (1998), and DeVries et al. (2006).

Spiral sculpture on specimens of *Scalina* is described according to a protocol previously employed with *Turritella* (Allmon, 1996; DeVries, 2007). Primary spiral cords are designated from anterior to posterior as 'E,' 'D,' 'C,' 'B,' and 'A' (Figure 2). Single or multiple secondary cords near the posterior suture are designated 'r,' 'rr,' 'rrr,' etc., and those near the anterior suture, 'w,' 'ww,' 'www,' etc. Secondary cords intercalated between primary spiral cords are designated in the following manner: EvDuCtBsA. Weak

primary spiral cords are listed in lower case; strong secondary cords are listed in upper case.

The principal shell characters used for distinguishing species of American *Scalina* include spire angle, whorl convexity, depth of suture, number of axial costae, lamellar extensions on costae, arrangement of primary spiral cords, presence of anterior ramping on primary spiral cords, complexity of secondary spiral cords, development of basal spiral cords, convexity of the basal region, and presence of a primary spiral cord bounding the basal region. The basal region may be entirely raised (a basal disk) or follow the contour of the anterior part of the body whorl.

Abbreviations for depositories for fossil specimens and localities are as follows: ANSP – Academy of Natural Sciences of Philadelphia, Pennsylvania, USA; FMNH – Florida Museum of Natural History, Gainesville, Florida, USA; LACM – Natural History Museum of Los Angeles County, California, USA; LACMIP – Natural History Museum of Los Angeles County, Invertebrate Paleontology; MUSM INV – Departamento de Paleontología de Vertebrados, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; OSU – Orton Museum, Ohio State University, Columbus, USA; PRI – Paleontological Research Institution, Ithaca, New

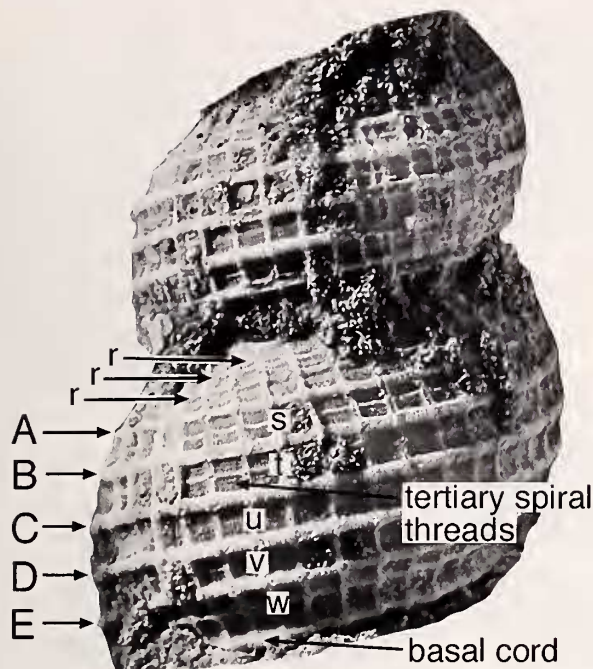


Figure 2. Arrangement and naming of spiral sculpture on *Scalina*. Primary spiral cords are labeled 'A,' 'B,' 'C,' 'D,' and 'E' between the posterior suture and anterior basal cord; intervening secondary spiral cords are labeled 'r,' 's,' 't,' 'u,' 'v,' and 'w' in the same direction.

York, USA; UCMP – University of California, Museum of Paleontology, Berkeley, USA; USGS – United States Geological Survey [Washington, D.C. register or Menlo Park, California, register (M series)]; many of the USGS specimens cited herein are now at UCMP; UWBM – Burke Museum of Natural History and Culture, University of Washington, Seattle, USA.

Museum numbers are followed by locality-sample numbers that are listed in the Appendix. Measurements of length (L) and width (W) are in millimeters. Numbers enclosed by parentheses indicate sizes for broken or deformed specimens. Specimens were coated with ammonium chloride prior to photography.

## SYSTEMATIC PALEONTOLOGY

### Family Epitoniidae S. S. Berry, 1910

#### Genus *Scalina* Conrad, 1865

Type species: (by subsequent designation, Palmer, 1937) *Scalina staminea* Conrad, 1865.

*Ferminoscala* Dall, 1908, p. 315.

**Discussion:** Some authors have assigned cancellate epitoniids with differentiated basal sculpture to *Amaea* (*Scalina*) [*Amaea* H. Adams & A. Adams, 1853; type

species by subsequent designation (Melville, 1897): *Scalaria magnifica* Sowerby II, 1844]. Data in this paper show that the diagnostic characters of *Scalina* have persisted within a monophyletic clade in the Americas since the early Miocene. It seems probable that the same characters unite a larger and more widely distributed group of Neogene *Scalina* species that is rooted in the Eocene, from which epoch numerous species of *Scalina* have also been identified (e.g., for the Americas, Durham, 1937; Weaver, 1942; MacNeil & Dockery, 1984). Because of the persistence of diagnostic characters, the longevity of the taxon, and its species richness, *Scalina* is herein assigned full generic rank, as has been done by others (e.g., Woodring, 1959; Olsson, 1964; Addicott, 1970; MacNeil & Dockery, 1984).

#### *Scalina ferminiana* (Dall, 1908)

Figures 3, 4, 6, 8–11

*Epitonium* (*Ferminoscala*) *ferminianum* Dall, 1908, p. 316, pl. 8, fig. 8.

*Epitonium* (*Ferminoscala*) *ferminianum* Dall. Olsson, 1942, p. 76, pl. 9, fig. 6.

*Scalina ferminiana* (Dall). Olsson, 1964, p. 200, pl. 33, figs. 2, 2a.

*Amaea* (*Scalina*) *ferminiana* (Dall, 1908). DuShane, 1974, p. 53, figs. 65, 68.

*Amaea* (*Scalina*) *ferminiana* (Dall, 1908). Peña, 1976, p. 2, fig. 2.

*Amaea* (*Scalina*) *ferminiana* (Dall, 1908). DeVries, 1986, p. 535, pl. 28, fig. 16.

*Amaea* (*Scalina*) *ferminiana* (Dall, 1908). DuShane, 1988, p. 53, figs. 2, 3.

*Amaea* (*Scalina*) *ferminiana* (Dall). Alamo & Valdivieso, 1997, p. 26, fig. 68.

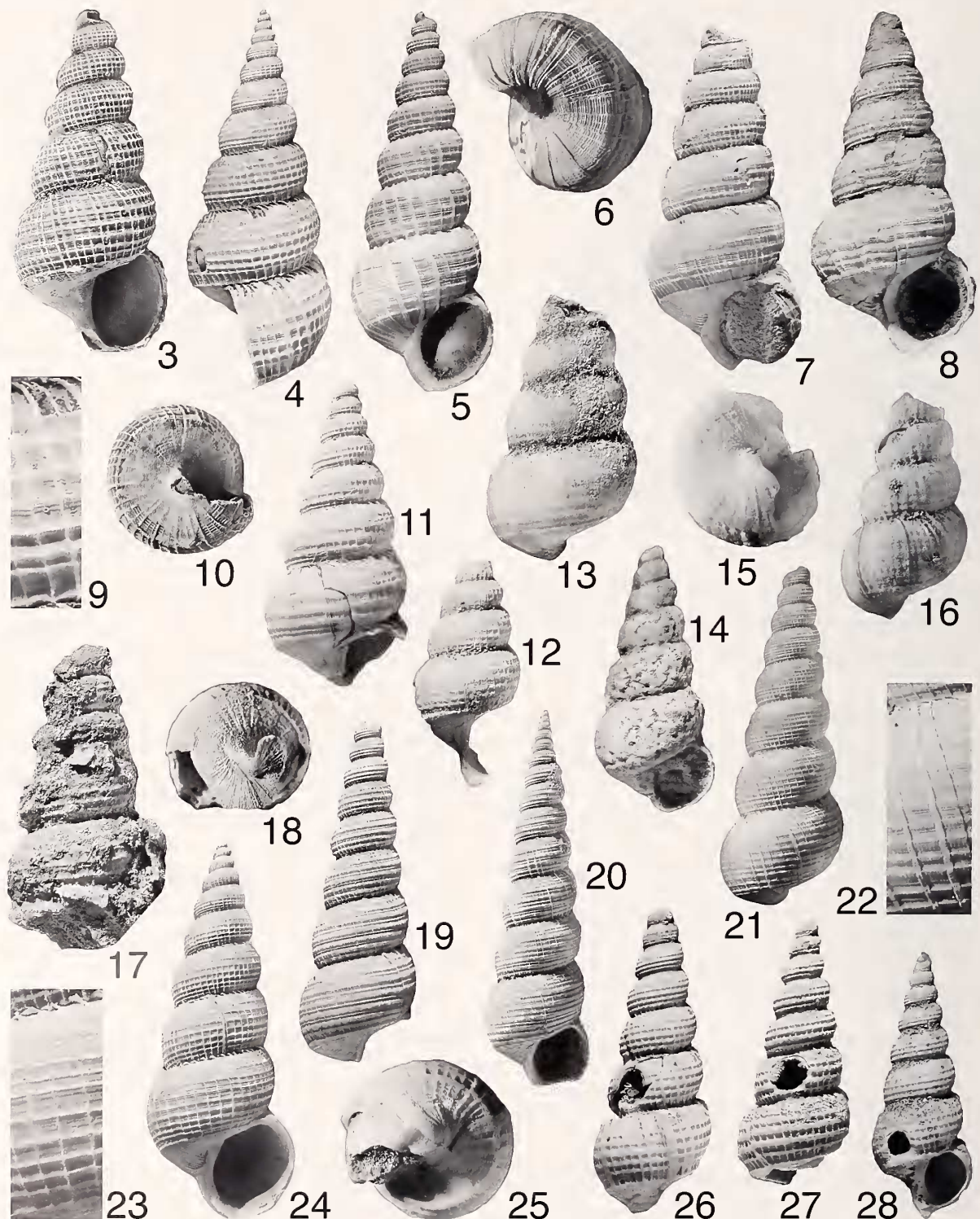
*Scala* (*Acrilla*) *weigandi* Böse, 1910, p. 259, pl. 12, fig. 8. Not *Scalina weigandi* (Böse). Woodring, 1959, p. 187, pl. 29, figs. 7, 8 (= *Scalina* aff. *S. isaacsoni*, sp. nov.).

*Epitonium* (*Ferminoscala*) *manabianum* Pilsbry & Olsson, 1941, p. 37, pl. 2, fig. 3.

**Diagnosis:** Shell length to 80 mm. Spire angle 24 to 26 degrees. Weakly and irregularly reticulate. Primary spiral cords ramped anteriorly. Basal disk not bounded by primary spiral cord.

**Description:** Shell length to 80 mm. Spire angle 24 to 26 degrees. Whorls moderately convex, shoulder evenly rounded; sutures moderately impressed. Protoconch not seen. Teleoconch of 13 whorls. Sculpture weakly reticulate, spiral elements stronger. Axial sculpture of 50 to 80 subequally spaced thin costae; a few irregularly spaced costae thickened. Costae stand well below spiral cords; slightly lamellate at posterior suture. Adult spiral formulae EDCBAr, wwEDCBArRrr, wEDC-





Figures 3, 4, 6, 8-11. *Scalina ferminiana* (Dall, 1908). Figure 3. LACMIP 7630. Pliocene, Ecuador. Apertural view. Length is 16.1 mm. Figure 4. PRI 4065. Panama, Pliocene-Pleistocene. Lateral view. Length is 41.1 mm. Figure 6. OSU 37549, DV 267-3. Northern Peru, Pliocene. Oblique view of base. Width is 15.4 mm. Figure 8. OSU 37548, DV 267-3. Apertural view. Length is 53.7 mm. Figure 9. PRI 4065. Close-up of sculpture showing anterior ramps and overlay of tertiary spiral threads on primary spiral



BARrrr, or wEDCBAr. Primary spiral cords evenly spaced, except 'D' closer to 'E.' Spiral cords ramped anteriorly and steeply rounded posteriorly. Interspaces with strong tertiary spiral threads, often superimposed upon primary spiral cords; interspaces also with tertiary axial threads. Basal disk present, weakly to moderately inclined, planar, with 30 closely spaced secondary spiral threads, extensions of weak costae, and tertiary spiral and axial threads; not bounded by primary spiral cord. Aperture ovate, moderately spatulate at base of columella; outer lip variably thickened. Umbilicus absent.

**Type Locality:** U.S.S. 'Albatross' station 2834, off Baja California, 87 m, mud bottom. Recent.

**Discussion:** Pliocene specimens of the Ecuadorian *Epitonium* (*Ferminoscala*) *manabianum* are placed in synonymy with *Scalina ferminiana*, as is the middle Pliocene (Akers, 1981) holotype of *S. weigandi* from the Caribbean side of the Isthmus of Tehuantepec, Mexico, because of their wide spire angles, anteriorly ramped spiral cords, and tertiary spiral threads incised prominently over the primary spiral cords. Specimens of *S. pseudoleroyi* (Maury, 1925) from the upper Pliocene Bowden Formation of Jamaica (Woodring, 1928; Pickerill et al., 1998) and upper Miocene Gatun beds of Panama (Woodring, 1959; Coates et al., 1992) typically have narrower spire angles than specimens of *S. ferminiana* and have a more complex differentiation of primary and secondary spiral cords. Specimens of the Recent Atlantic *S. mitchelli* are similar in size and shape to those of *S. ferminiana*, but have stronger and fewer axial costae and a spiral band of brown that is

not present on equally well preserved Recent specimens of *A. ferminiana*.

Individuals of *Scalina ferminiana* presently live at shelf depths from Baja California to Paita, Peru (DuShane, 1974; Peña, 1976; Alamo & Valdivieso, 1997). Examples in LACM collections obtained live and dead between 15°58'N and 4°57'S were nearly always found on soft sediment at water depths greater than 36 m. Pliocene individuals from the Esmeraldas beds of Ecuador, Tehuantepec outcrops of southern Mexico, and Charco Azul outcrops of Panama occupied deep-water environments (Olsson, 1942, 1964; DuShane, 1988). Specimens from the upper Pliocene or Pleistocene Canoa Formation of Ecuador came from mid-shelf depths (Pilsbry & Olsson, 1941; Bianucci et al., 1997; Collins, 2006). Upper Pliocene specimens from the Taime Formation of northern Peru, in contrast, were found in fine-grained sandstones once deposited in a lagoon (DeVries, 1986, 1988).

**Material:** ANSP 13641, holotype, *Epitonium* (*Ferminoscala*) *manabianum* Pilsbry & Olsson, 1941, Ecuador, Pliocene, L (37.7), W (17.9); LACMIP 7631, LACMIP locality 11794, Ecuador, Pliocene, L (24.9), W 10.8; LACMIP 7630, hypotype, LACMIP locality 11794, L 16.1, W 7.3; OSU 37548, DV 267-3, northern Peru, late Pliocene to early Pleistocene, L 53.7, W 25.7; OSU 37549, DV 267-3, L 33.4, W 15.4; OSU 37550, DV 236-3, northern Peru, late Pliocene to early Pleistocene, L (41), W (22); PRI 4065, Panama, Pliocene to Pleistocene, L 41.1, W (15.4).

**Occurrence:** Late Pliocene: Southern Mexico (Caribbean); Panama to Ecuador and northern Peru. Recent: Gulf of California to northern Peru.

cords. Figure 10. LACMIP 7630. Basal view. Width is 7.3 mm. Figure 11. ANSP 13641. Holotype of *Epitonium* (*Ferminoscala*) *manabianum* Pilsbry & Olsson, 1941. Ecuador, Pliocene. Apertural view. Outer lip is missing. Length is 37.7 mm.

Figure 5. *Scalina mitchelli* (Dall, 1896). FMNH 00128594, Texas, Recent. Apertural view. Medial brown band visible beneath light coating of ammonium chloride. Length is 47.1 mm.

Figure 7. *Scalina pseudoleroyi* (Maury, 1925). USNM 562623, USGS locality 8410. Panama Canal Zone, Pliocene. Apertural view. Length is 35.5 mm.

Figures 12–18. *Scalina cheneyi*, sp. nov. Figure 12. UWM 98094, DV 571-6, syntype. Southern Peru, late Miocene. Apertural view, outer lip missing. Length is 12.2 mm. Figure 13. MUSM INV 144, DV 571-6, syntype. Abapertural view. Length is 16.2 mm.

Figure 14. UWM 98095, DV 599-2. Southern Peru, late Miocene. Apertural view, replaced with gypsum and severely pitted. Length is 24.0 mm. Figure 15. MUSM INV 145, DV 571-6. Basal view. Width is 5.9 mm. Figure 16. UWM 98092, DV 571-6. Abapertural view. Length is 12.8 mm. Figure 17. MUSM INV 146, DV 523-2. Southern Peru, early Pliocene. Lateral view. Length is 32.2 mm. Figure 18. UWM 98094. Basal view. Width is 5.6 mm.

Figures 19–22. *Scalina brunneopicta* (Dall, 1908). Figure 19. ANSP 13640, holotype of *Epitonium eleutherium* Pilsbry & Olsson, 1941. Ecuador, Pliocene. Apertural view, outer lip and columella missing. Length is 21.1 mm. Figure 20. LACM 127965. Mexico, Recent. Apertural view. Length is 36.8 mm. Figure 21. LACM 38-8. Mexico, Recent. Abapertural view. Length is 32.1 mm. Figure 22. LACM 38-8. Close-up of sculpture.

Figures 23, 24. *Scalina tehuancarum* (DuShane & McLean, 1968). Figure 23. LACM 1162, holotype. Mexico, Recent. Close-up of sculpture. Figure 24. LACM 1162. Apertural view. Length is 39.5 mm.

Figures 25–28. *Scalina whitei* (Keen, 1943). Figure 25. USGS M2480, specimen 1. California, middle Miocene. Basal view. Width is 8.0 mm. Figure 26. USGS M2480, specimen 1. Abapertural view. Length is 21.3 mm. Figure 27. UCMP B1638, specimen 15430. California, middle Miocene. Abapertural view. Length is 12.9 mm. Figure 28. USGS M1613, specimen 1. California, middle Miocene. Apertural view. Length is 16.7 mm.

*Scalina mitchelli* (Dall, 1896)

## Figure 5

*Scala mitchelli* Dall, 1896, p. 112.

*Amaea* (*Amaea*) *mitchelli* (Dall). Clench & Turner, 1950, p. 243, pl. 106, figs. 5–7.

*Amaea mitchelli* (Dall). Princz, 1982, p. 174–175.

**Diagnosis:** Shell length to 65 mm. Spire angle 20 to 26 degrees. Axial costae strong, irregularly thickened; fewer than 45 on body whorl. Primary spiral cords ramped anteriorly; intercalated secondary spiral cords often present.

**Description:** Shell length to 65 mm. Spire angle 20 to 26 degrees. Whorls moderately convex, shoulders evenly rounded, sutures moderately impressed. Protoconch unknown. Teleoconch of 14 to 15 whorls; early whorls posteriorly angulate at periphery. Sculpture reticulate, axial elements as strong or stronger than spiral elements. Axial sculpture of 20 to 45 costae, several irregularly thickened, often slightly lamellose at posterior suture. Adult spiral formula wEDuCBarr or with additional intercalated strong secondary spiral cords and strong tertiary threads; spacing of primary spiral cords subequal. Primary spiral cords ramped usually anteriorly. Basal disk present, moderately inclined, planar to slightly convex, with about 20 to 40 closely spaced mixed secondary spiral cords and tertiary spiral threads, and strong extensions of axial costae; bounded by 1 to 3 flattened primary spiral cords or unbounded. Aperture ovate, spatulate at base of columella. Outer lip sometimes thickened. Umbilicus absent. Whorls with medial brown band, one-third of whorl's axial length, and brown basal disk.

**Type Locality:** Beach drift, Matagorda Island, Texas. Recent.

**Discussion:** *Scalina mitchelli* is sometimes placed in *Amaea* (*Amaea*) (e.g., Clench & Turner, 1950), but its differentiated basal region, clearly noted by Dall (1896), places it with *Scalina* (DuShane, 1974; MacNeil & Dockery, 1984). Specimens of *S. mitchelli* have fewer and coarser axial costae than either *S. ferminiana* or a similar fossil species, *S. pseudoleroyi*, but as many intercalated secondary spiral cords as specimens of the latter species.

**Material:** FMNH 145466, Gulf of Mexico, Mexico, Recent, L (49.6), W 20.5; W 17.4; FMNH 152778, Gulf of Mexico, Mexico, Recent, L 57.0, W 18.5; FMNH 00128594, Texas, Recent, L 47.1.

**Occurrence:** Recent: Gulf of Mexico, Caribbean, Venezuela (Princz, 1982).

*Scalina pseudoleroyi* (Maury, 1925)

## Figure 7

*Epitonium* (*Acrilla*) *pseudoleroyi* Maury, 1925, p. 243.

*Ferminoscala pseudoleroyi* (Maury). Woodring, 1928, p. 402, pl. 32, figs. 3, 4.

*Scalina pseudoleroyi* (Maury). Woodring, 1959, p. 187, pl. 38, figs. 6, 21.

Not *Scalina pseudoleroyi* (Maury). Jung, 1965, p. 493, pl. 65, fig. 6 (= *Scalina belti*, sp. nov.).

*Scalaria leroyi* Guppy. Guppy 1874, p. 406, pl. 16, fig. 10. Not pl. 18, fig. 2.

Not *Scalaria leroyi* Guppy, 1867, p. 168.

**Diagnosis:** Shell length about 40 mm. Spire angle about 20 degrees. Primary spiral cords ramped anteriorly; tertiary spiral threads encroach upon primary spiral cords; some intercalated secondary spiral cords. Basal disk not bounded by spiral cord.

**Description:** Shell length about 40 mm. Spire angle about 20 degrees. Whorls moderately convex, shoulder evenly rounded, sutures moderately impressed. Protoconch unknown; broken teleoconch of at least six whorls. Sculpture moderately reticulate. Axial sculpture of 40 to 70 costae standing slightly above primary spiral cords; some cords lamellate, especially at posterior suture; others thickened at irregular intervals. Spiral formula wwWEDCBsArrrr; primary spiral cords evenly spaced; interspace between 'E' and anterior suture broad. Primary spiral cords thin, ramped anteriorly. Strong tertiary spiral threads intercalated with and encroaching upon primary spiral cords. Basal disk moderately inclined, planar or slightly convex, with about 25 to 30 closely spaced secondary spiral cords; also with extensions of axial costae; not bounded by primary spiral cord. Aperture ovate, slightly spatulate at base of columella. Umbilicus absent.

**Type Locality:** Jamaica. Pliocene.

**Discussion:** As noted by Woodring (1959), the Gatun specimens of *Scalina pseudoleroyi* are more similar to the eastern Pacific *S. ferminiana* than either Recent Atlantic species (*S. mitchelli*, *S. retifera*) assigned to *Scalina*, differing from *S. ferminiana* by having a narrower spire angle, more prominent axial costae, and weaker primary spiral cords. The spiral sculptural pattern is very much like that of *S. teluanarum*, but the latter species has many fewer basal secondary spiral cords and a spire that uniquely among *Scalina* species changes its angle along its length.

**Material:** USNM 562623, USGS locality 8410, Panama, Pliocene, L (35.5), W 15.4; USNM 115437, holotype, Jamaica, Pliocene, L (25.3), W 13.4.

**Occurrence:** Pliocene: Caribbean.



*Scalina cheneyi*, sp. nov.

## Figures 12–18

**Diagnosis:** Spire angle about 21 degrees. Primary spiral cords low, broad, wider than interspaces. Basal disk not bounded by spiral cord.

**Description:** Shell length to 50 mm. Spire angle 21 degrees. Whorls moderately and evenly convex, sutures moderately impressed. Protoconch unknown. Spire incomplete; teleoconch with at least six whorls. Sculpture subdued; spiral elements stronger. Axial sculpture of 44 to 55 costae; costae rise slightly above spiral cords, with lamellar extensions sometimes present at one or both sutures. Spiral formula wEDuCBAr, also wwEDCBAr. Primary spiral cords low, broad, sometimes anteriorly ramped, wider than interspaces; unevenly spaced, 'D' closer to 'E.' Basal disk present, with about 12 secondary spiral threads; not bounded by primary spiral cord. Aperture oval to almost circular; base of columella / inner lip slightly spatulate. Outer lip thin. Umbilicus absent.

**Type Locality:** DV 571-6, Alto Grande, at the northern edge of the Sacaco Basin, southern Peru, in a sublittoral shell lag or intertidal beach deposit near the base of the Pisco Formation (Figure 29). Lower upper Miocene.

**Discussion:** Specimens of late Miocene and early Pliocene *Scalina cheneyi* differ from those of the younger *S. ferminiana* by having a narrower spire, deeper sutures, and broad primary spiral cords with less well-developed tertiary spiral threads. They differ from specimens of the middle Miocene Peruvian *S. isaacsoni* and all older Neogene Peruvian species by lacking sharply rounded, widely spaced spiral cords and by having a larger spire angle. The broad spiral cords of *S. cheneyi* resemble those on specimens of Recent *S. brunneopicta*, although specimens of the latter have many more primary spiral cords and a much narrower spire angle.

**Etymology:** Named for Jack Cheney, the author's professor of igneous and metamorphic petrology at Amherst College in 1976.

**Material:** MUSM INV 144, DV 571-6, syntype, Peru, late Miocene, L (16.2), W 9.1; MUSM INV 145, DV 571-6, syntype, L (9.6), W 5.9; MUSM INV 146, DV 523-2, Peru, early Pliocene, L (32.2), W 14.4; UWBM 98092, DV 571-6, syntype, L (12.8), W (6.7); UWBM 98093, DV 571-6, syntype, L (19.1), W (8.3); UWBM 98094, DV 571-6, syntype, L (12.2), W (5.6); UWBM 98095, DV 599-2, Peru, late Miocene, L (24.0), W 10.7; UWBM 98096, DV 599-2, L (14.6), W 8.5; UWBM 98097, DV 599-2, lot of 11; UWBM 98098, DV 523-2, L (32.9), W 15.2; UWBM 98099, DV 523-4, Peru, early

Pliocene, L (27.0), W (11.3); UWBM 98106, DV 1348-1, southern Peru, late Miocene, L (18.2), W 8.9.

**Occurrence:** Early late Miocene to early Pliocene: southern Peru.

*Scalina brunneopicta* (Dall, 1908)

## Figures 19–22

*Epitonium* (*Ferminoscala*) *brunneopictum* Dall, 1908, p. 316, pl. 8, fig. 10.

*Antaea* (*Scalina*) *brunneopicta* (Dall, 1908). DuShane, 1974, p. 53, figs. 63, 64, 68.

*Antaea* (*Scalina*) *brunneopicta* (Dall, 1908). DuShane, 1979, p. 97, figs. 3, 4.

*Scalina* cf. *S. brunneopicta* (Dall). Woodring, 1959, p. 188, pl. 38, figs. 7, 14.

*Epitonium* (*Ferminoscala*) *eleutherium* Pilsbry & Olsson, 1941, p. 38, pl. 2, fig. 7.

(?) *Scalina mitchelli* (Dall). Perrilliat, 1972, p. 53, pl. 25, figs. 8–13.

**Diagnosis:** Spire angle about 14 degrees. Costae irregularly thickened, not lamellar. Primary and secondary spiral cords equally strong, broad or asymmetrically triangular.

**Description:** Shell length to 44 mm. Spire angle about 14 degrees. Whorls weakly convex, shoulder steeply inclined, sutures weakly to moderately impressed. Protoconch unknown. Teleoconch of 13 to 14 whorls. Sculpture very weakly reticulate. Axial sculpture of 40 to 45 thin, unevenly spaced costae barely standing as high as spiral cords except several irregularly spaced thickened costae. Costae slightly extended at posterior suture. Earliest teleoconch whorl posteriorly angulate with spiral formula bCd; subsequent whorls with spiral formulae edCb, EDCBa, wEDCBa, wEDuCBAr, WEvDuCtBsAr, and on body whorl, WEvDUCTBsArr; also WEVDUCTBAr. Primary spiral cords evenly spaced. Spiral cords broad and flattened or anteriorly ramped; as wide or wider than interspaces. Interspaces with tertiary spiral threads and very faint axial threads. Basal disk nearly fully formed, moderately inclined, planar, with 12 to 16 closely spaced secondary spiral cords and intervening tertiary spiral threads, extensions of costae, and axial threads; bounded by weak spiral cord. Aperture ovate, weakly to moderately spatulate at base of columella. Outer lip thin. Umbilicus absent.

**Type Locality:** U.S.S. 'Albatross' station 2835, 10 m water depth, mud bottom, off Baja California. Recent.

**Material:** LACM 127965, Sonora, Mexico. Recent, L 36.8, W 10.0; LACM 38-8, Guerrero, Mexico, Recent, specimen 1, L 32.1, W 11.2; LACM 38-8, specimen 2, L

29.0, W 9.1; ANSP 13640, holotype of *Epitotium eleutherium* Pilsbry & Olsson, 1941, Ecuador, Pliocene, L 21.1, W 6.9.

**Discussion:** The Pliocene Ecuadorian *Epitotium eleutherium* does not differ in any significant respect from specimens of Recent *Scalina brunneopicta* in LACM collections and so is considered a junior synonym of the latter species. The small specimens of late Miocene *Scalina* cf. *S. brunneopicta* Woodring, 1959, from the upper Gatun Formation of Panama have broad primary spiral cords but lack the intercalation of strong secondary with primary spiral cords seen on adult specimens of *S. brunneopicta*; they may be juveniles. Specimens from the middle Pliocene Agueguexquite Formation of Mexico (Perrilliat, 1972; Akers, 1981) are more elongate than those of *S. mitchelli*, to which they were assigned; they are more similar to specimens of *S. brunneopicta*.

**Occurrence:** Late Miocene: Panama: Pliocene: Southern California to Ecuador. Recent: Gulf of California and Baja California to Ecuador.

*Scalina teluanarum* (DuShane & McLean, 1968)

Figures 23, 24

*Anaea (Scaliua) teluanarum* DuShane & McLean, 1968, p. 4, figs. 4, 5.

*Anaea (Scalina) teluanarum* DuShane & McLean, 1968. DuShane, 1974, p. 56, fig. 68.

*Anaea (Scalina) teluanarum* DuShane & McLean, Alamo & Valdivieso, 1997, p. 26.

*Anaea (Scaliua) teluanarum* DuShane & McLean, 1968. Weil et al., 1999, fig. 445.

**Diagnosis:** Spire angle varies along length of shell. Body whorl with eight to nine strong spiral cords, spaced at diminishing intervals anteriorly. Outer lip thickened.

**Description:** Shell length to 50 mm. Spire angle varies from 25 degrees posteriorly to 20 degrees anteriorly. Whorls weakly to moderately convex, shoulder short, weakly tabulate, sutures weakly impressed. Protoconch unknown. Teleoconch of at least nine whorls. Sculpture moderately reticulate. Axial sculpture of 47 equally spaced thin costae standing slightly higher than spiral cords; several costae thickened at irregular intervals. Costae often extended adapically at posterior suture. Earliest visible whorl angulate with spiral formula edcB, followed by edcBa, wEDCBarr, wWEDCBARR, and on body whorl, wWEDuCbArrRrrr. Primary spiral cords rounded, ramped anteriorly, evenly spaced on periphery, increasingly closely spaced anteriorly. Interspaces with strong tertiary spiral threads and obsolete axial threads. Basal disk partly formed; basal region steeply

inclined, convex, with 12 evenly spaced secondary spiral cords and extensions of costae; interspaces with axial threads and obsolete spiral threads; bounded by weak spiral cord. Aperture oval, moderately spatulate at base of columella. Outer lip thickened. Umbilicus absent.

**Type Locality:** Gulf of Tehuantepec, Mexico, 59 to 68 m water depth, mud bottom. Recent.

**Discussion:** The shape of the primary spiral cords, the coarseness of the secondary spiral cords on the basal region, and adapical extension of costae at the shoulder on the holotype of *Scaliua teluanarum* is like that on specimens of *S. brunneopicta*. The large spire angle is like that of *S. feruinaua*, although the spire of *S. teluanarum* is uniquely bowed.

**Material:** LACM 1162, holotype, Mexico, Recent, L 39.5, W 14.9.

**Occurrence:** Recent: Gulf of California to northern Peru (DuShane, 1974; Alamo & Valdivieso, 1997; Weil et al., 1999).

*Scalina whitei* (Keen, 1943)

Figures 25–28

*Feruinoscala whitei* Keen, 1943, p. 46, pl. 4, figs. 32, 33. *Scaliua whitei* (Keen). Addicott, 1970, p. 56, pl. 3, figs. 20, 25–28.

*Feruinoscala durhami* Keen, 1943, p. 46, pl. 4, fig. 31. *Scaliua durhami* (Keen). Addicott, 1970, p. 56, pl. 3, figs. 21, 24.

Not *Acrilla* (*Feruinoscala*) *durhami* Zinsmeister, 1983, p. 1291, figs. 2N, 2O.

(?) *Scaliua* sp. Perrilliat, 1992, p. 23, pl. 7, fig. 1.

**Diagnosis:** Shell length to 24 mm. Shoulder steeply inclined. Primary spiral cords broad, sometimes thickened; often intercalated with secondary primary cords. Basal region with eight secondary spiral cords.

**Description:** Shell length to 24 mm. Spire angle 19 to 21 degrees. Whorls moderately convex; sutures moderately impressed; shoulder broad, steeply inclined. Protoconch unknown. Teleoconch of 13 whorls; sculpture strongly reticulate. Axial sculpture of 42 to 45 thin costae, uniformly spaced and level with spiral cords, occasionally thick and standing above spiral cords. Costae often with small, adaxially hooked, recurved or upright extensions on shoulder. Spiral sculpture wEDCBarr, EDCBARR, or wEvDuCbArrrr (hypotype); 'r' and 'A' on shoulder. Primary spiral cords 'A,' 'B,' 'C,' 'D,' and 'E' thick, evenly convex or flattened, width variable; 'B,' 'C,' and 'D' strongest. Interspaces with minute reticulation of spiral and axial threads. Basal disk absent; basal region steeply in-





Figure 29. Type locality (DV 571-6) of *Scalina cheneyi*, sp. nov., along Panamerican Highway near Alto Grande, southern Peru.

clined, planar, with eight secondary spiral cords, extensions of axial costae, and minute tertiary spiral and axial threads; bounded by strong primary spiral cord. Aperture ovate, slightly spatulate anterior to columella. Outer lip thin. Umbilicus absent.

**Type Locality:** LSJU locality 2121, six miles northeast of Edison, California. Round Mountain Silt, middle Miocene.

**Discussion:** Specimens of *Scalina whitei* are smaller than those of *S. isaacsoni*, slightly broader, with whorls that are more convex and spiral cords that are usually more closely spaced. The spiral sculptural formula of *S. whitei* is usually as simple as that of *S. isaacsoni*, although the hypotype shows a more complex spiral pattern reminiscent of early Miocene species of *Scalina* in southern Peru. *Scalina durhami* (Keen, 1943) appears to be a worn example of *S. whitei* from the same locality.

Specimens of *Scalina whitei* were collected by Keen (1943) and Addicott (1970) from the deep-water Olcese Sandstone and Round Mountain Silt of central California, units recently assigned ages of late early

Miocene and early middle Miocene, respectively (Sanchez, 2003). A poorly preserved specimen of *Scalina* from the middle Miocene Ferrotepec Formation on the central Pacific coast of Mexico (Perrilliat, 1992) may be referable to *S. whitei* or the middle Miocene Peruvian *S. isaacsoni*.

**Material:** (all material from California, middle Miocene) UCMP specimen 15430, UCMP B1638, L 12.9, W 5.7; UCMP B1601, lot of 1; USGS 6064, lot of 2; USGS M1608, lot of 1; USGS M1613, specimen 1, L 16.7, W 6.2; USGS M1613, lot of 15; USGS M2480, specimen 1, L 21.3, W 8.0; USGS M2480, lots of 3 and 4.

**Occurrence:** Early to middle Miocene: Southern California.

### *Scalina retifera* (Dall, 1889)

Figures 30–34

*Scala (Acrilla) retifera* Dall, 1889, p. 312.

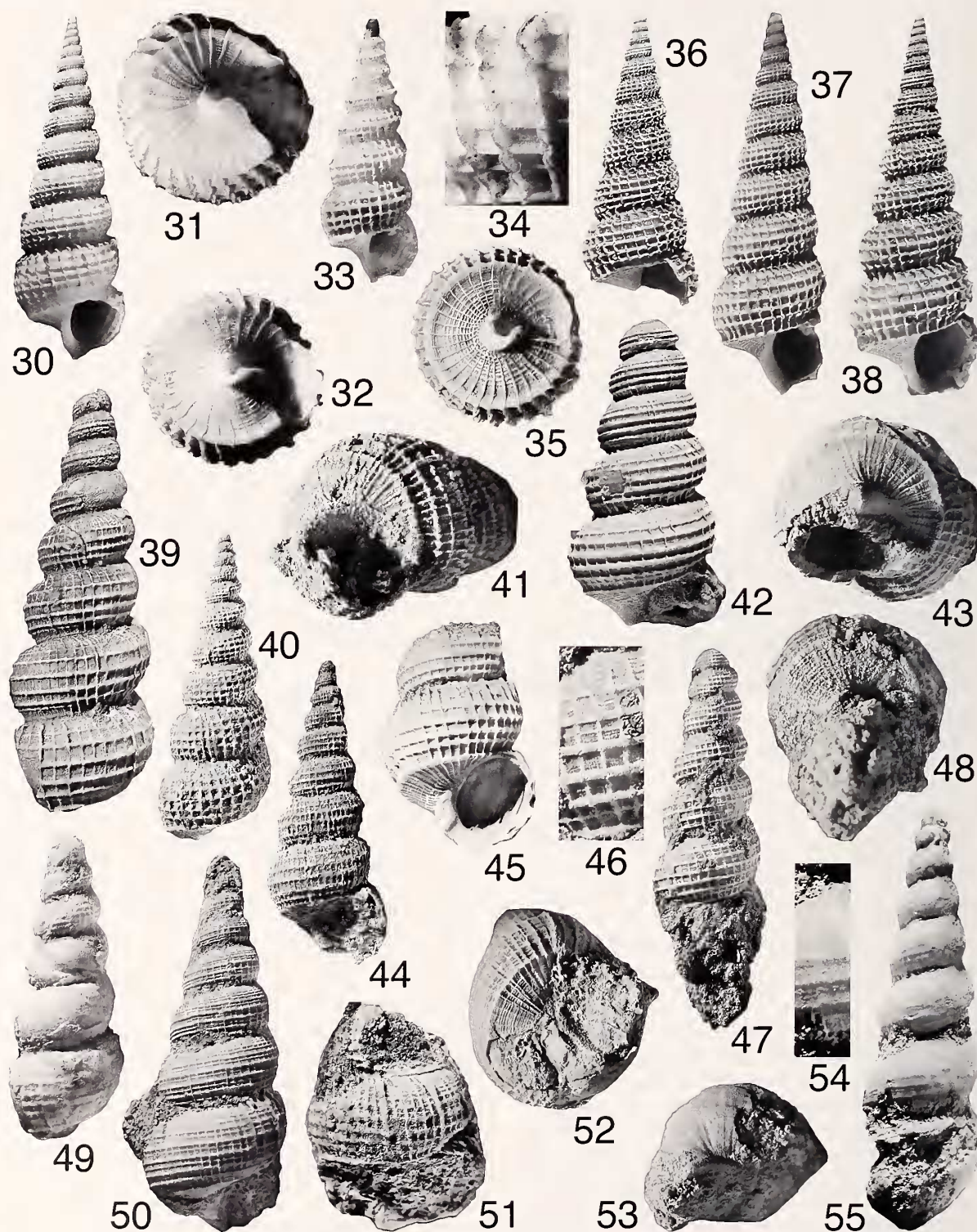
*Anaea (Feminoscala) retifera* Dall, Clench & Turner, 1950, p. 243, pl. 96; pl. 106, figs. 1–4.

*Anaea (Scalina) retifera* (Dall, 1889). Ríos, 1985, pl. 53, fig. 745.

*Anaea retifera*. Ardovini & Cossignani, 2004, unnumbered figure, p. 137.

**Diagnosis:** Shoulder angulate, tabulate. Lamellar costae raised, extended adapically at shoulder. Secondary spiral cords between primary spiral cords generally absent.

**Description:** Shell length to 32 mm. Spire angle about 20 degrees. Whorls moderately convex, shoulder narrow, angulate, and slightly tabulate; sutures deeply impressed. Protoconch of three deviated translucent brown whorls with minute spiral and axial scratches. Teleoconch of 14 to 15 whorls; sculpture strongly reticulate. Axial sculpture of 26 to 30 evenly spaced, recurved, lamellar costae standing well above and scalloped across all spiral cords; costae weakly extended adaxially at shoulder. Earliest teleoconch whorl strongly angulate with spiral formula bCd. Subsequent whorls with spiral formulae edCb, eDCBa, eDCBa, EDCBa, wEDCBar, and wEDCBarr by sixth whorl. Body whorl with spiral formula wEDCBarr. Primary spiral cords evenly spaced; interspace between 'E' and anterior suture broad; 'B,' 'C,' and 'D' slightly stronger than 'A' and 'E.' Two secondary 'r' spiral cords very weak. Spiral cords raised, steeply rounded, half as wide as interspaces. Interspaces with spiral and axial tertiary threads. Basal disk absent; basal region weakly inclined, slightly concave, with about 30 tertiary spiral threads, extensions of axial costae, and minute tertiary axial threads; bounded by primary spiral cord.



Figures 30-34. *Scalina retifera* (Dall, 1889). Figure 30. LACM 164927, specimen 1. Florida, Recent. Apertural view. Length is 30.9 mm. Figure 31. LACM 164927, specimen 1. Basal view. Width is 9.7 mm. Figure 32. LACM 164927, specimen 2. Basal view. Width is 6.5 mm. Figure 33. DeVries collection, Panama (Caribbean), Recent. Apertural view showing deviated protoconch. Length is 6.7 mm. Figure 34. LACM 164927, specimen 1. Close-up of sculpture.



Aperture nearly circular, weakly spatulate anterior to columella. Outer lip thin. Umbilicus absent.

**Type Locality:** 27 to 40 km off the coast of North Carolina, U.S. Fish Commission Stations 2595 and 2596, in 89 to 115 m water depth; sand bottom. Recent.

**Material:** LACM 164927, Florida, Recent, specimen 1, L 30.9, W 9.7; LACM 164927, specimen 2, L 20.0, W 6.5; DeVries collection, Panama (Caribbean), Recent, L 6.7, W 2.2.

**Discussion:** The description of *Scalina retifera* by Clench and Turner (1950) is more detailed than that of Dall (1889) and consistent with the above description drawn from LACM material. The number of costae varies according to the size of the specimen but is less than the number seen on specimens of the Recent Pacific geminate species, *S. deroyae* or the middle Miocene Peruvian *S. isaacsoni*.

**Occurrence:** Recent: Gulf of Mexico, North Carolina to Brazil (Ríos, 1985) and West Africa (Weil et al., 1999; Ardovini & Cossignani, 2004).

*Scalina deroyae* (DuShane, 1970)

Figures 35–38

*Amaea (Scalina) deroyae* DuShane, 1970, p. 330, pl. 51, fig. 2.

*Amaea (Scalina) deroyae* DuShane, 1970. DuShane, 1974, p. 54, fig. 67.

**Diagnosis:** Shoulder rounded. Lamellar costae raised, radially extended posteriorly. Secondary cords weak or absent.

**Description:** Shell length to 22 mm. Spire angle 14 to 18 degrees. Whorls moderately convex, shoulder narrow,

steeply inclined; sutures weakly to moderately impressed. Protoconch unknown. Teleoconch of 14 whorls. Sculpture strongly reticulate. Axial sculpture of 31 to 34 upright to recurved lamellar costae standing above and scalloped across spiral cords; weakly extended radially or adapically at shoulder. Earliest teleoconch whorl evenly rounded with spiral formula bCd. Subsequent whorls with spiral formulae edCb, eDCBa, and wEDCBA. Body whorl with spiral formulae wEDCBA, wEDCBAr, or EDCBA; secondary cords 'r' and 'w' weakly developed or absent. Primary spiral cords evenly spaced, all nearly equal in size; interspace between 'E' and anterior suture not much broader than other primary spiral cord interspaces. Spiral cords steeply rounded, elevated, half as wide as interspaces. Interspaces with fine reticulation of tertiary spiral and axial threads. Basal disk absent; basal region weakly inclined, planar to deeply concave, with about nine secondary spiral cords closest to axis, intervening tertiary spiral threads, extensions of axial costae, and axial threads; bounded by strong primary spiral cord. Aperture ovate, nearly circular, weakly spatulate near columella. Outer lip thin. Umbilicus absent.

**Type locality:** Tagus Cove, Isla Isabela (Albemarle), Islas Galapagos, cruise of R/V Velero III, 55 m water depth, rock and coral bottom. Recent.

**Material:** LACM 1236 (AHF 147-34), holotype, Ecuador, Recent, L 22.6, W 6.6; LACM 128144, Mexico, Recent, L 19.8, W 6; LACM 55642, Mexico, Recent, specimen 1, L 14.0, W 4.5; LACM 55642, specimen 2, L (10.5), W 4.1; LACM 55642, specimen 3, L 22.4, W 7.1.

**Discussion:** Specimens of *Scalina deroyae* are similar to those of *S. retifera*, but are slightly narrower, have less

Figures 35–38. *Scalina deroyae* (DuShane, 1970). Figure 35. LACM 55642, specimen 3. Mexico, Recent. Basal view. Width is 7.1 mm. Figure 36. LACM 55642, specimen 2. Apertural view, body whorl broken. Length is 10.5 mm. Figure 37. LACM 55642, specimen 3. Apertural view. Length is 22.4 mm. Figure 38. LACM 128144, Mexico, Recent. Apertural view. Length is 19.8 mm. Figures 39–44. *Scalina isaacsoni*, sp. nov. Figure 39. UWB 98107, DV 1655-4, syntype. Southern Peru, middle Miocene. Lateral view. Length is 40.7 mm. Figure 40. UWB 98110, DV 1655-3, syntype. Southern Peru, middle Miocene. Abapertural view. Length is 18.6 mm. Figure 41. UWB 98109, DV 1653-1, syntype. Southern Peru, middle Miocene. Oblique basal and apertural view. Width is 11.0 mm. Figure 42. MUSM INV 150, DV 1655-4, syntype. Apertural view, outer lip and columella missing. Length is 29.5 mm. Figure 43. UWB 98107. Oblique view of base. Width is 14.5 mm. Figure 44. MUSM INV 151, DV 1655-3, syntype. Apertural view. Length is 20.1 mm. Figure 45. *Scalina* aff. *S. isaacsoni*, sp. nov. [= *S. weigandi* (Böse, 1910) of Woodring, 1959, not Böse, 1910 (= *S. ferminiana*)]. USNM 562642, USGS locality 16937, Panama, late Miocene to early Pliocene. Length is 20.4 mm. Figures 46–48. *Scalina belti*, sp. nov. UWB 98100, DV 575-3, holotype. Southern Peru, late early Miocene. Figure 46. Close-up of sculpture showing medial secondary spiral cords. Figure 47. Lateral view. Length is 23.0 mm. Figure 48. Basal view. Figures 49–52. *Scalina brophyi*, sp. nov. Figure 49. MUSM INV 148, DV 478-3, paratype. Southern Peru, early Miocene. Abapertural view. Length is 31.8 mm. Figure 50. UWB 98101, DV 478-3, holotype. Apertural view, outer lip missing. Length is 48.6 mm. Figure 51. UWB 98102, DV 478-3, paratype. Lateral view of one whorl. Length is 13.1 mm. Figure 52. UWB 98101. Oblique basal view. Width is 18.0 mm. Figures 53–55. *Scalina foosei*, sp. nov. UWB 98104, DV 1123-1, holotype. Southern Peru, late Eocene. Figure 53. Basal view. Width is 9.1 mm. Figure 54. Close-up of sculpture. Figure 55. Lateral view. Length is 32.5 mm.

impressed sutures and less tabulate shoulders, more costae per whorl, more uniformly developed primary spiral cords, less well developed secondary spiral cords, and spiral cords that are more differentiated in size on the basal region.

**Occurrence:** Recent: Mexico to Ecuador.

*Scalina isaacsoni*, sp. nov.

Figures 39–44

**Diagnosis:** Shell length to 50 mm. Spire angle 16 to 19 degrees; whorls strongly convex. Sculpture strongly reticulate. Primary spiral cords narrow, elevated, rounded. Secondary cords absent between primary spiral cords.

**Description:** Shell length to 50 mm. Spire angle 16 to 19 degrees. Whorls strongly convex, slightly angulate posterior to midpoint; sutures deeply impressed; shoulder broad, steeply inclined. Protoconch unknown. Teleoconch of 14 to 15 whorls; sculpture strongly reticulate. Axial sculpture of 34 to 36 weakly scalloped costae on largest body whorls, more costae on earlier whorls. Costae thin, some thickened and standing above spiral sculpture, some slightly extended radially or adapically. Earliest teleoconch whorl posteriorly angulate with spiral formula dCB; subsequent whorls with spiral formulae EDCB, EDCBa, EDCBArr, and on body whorl, usually wEDCBArr, or less often, EDCBAr. Primary spiral cords evenly spaced; interspace between spiral cord 'E' and anterior suture similarly separated; 'B,' 'C,' and 'D' are larger. Spiral cords steeply rounded, elevated, half as wide as interspaces or narrower. Interspaces with reticulation of tertiary spiral and axial threads. Basal disk absent; basal region moderately inclined, planar, with about ten to 14 low secondary spiral cords, intervening tertiary spiral threads, extensions of axial costae, and axial threads; bounded by strong primary spiral cord. Aperture nearly circular, weakly spatulate near columella. Outer lip thin. Umbilicus absent.

**Type Locality:** DV 1655-4, west face of small ridge, lower Ica valley, 14 m up in measured section, thin sandstones interpreted to be deposited in a large embayment (Figure 56). Pisco Formation. Middle Miocene.

**Etymology:** Named for Peter E. Isaacson, the author's senior thesis advisor at Amherst College from 1976 to 1977.

**Discussion:** Specimens of *Scalina isaacsoni* resemble those of the Recent Atlantic *S. retifera* and Pacific *S. deroyae*. Adult specimens of both Recent species, however, are half the length of the largest of *S.*

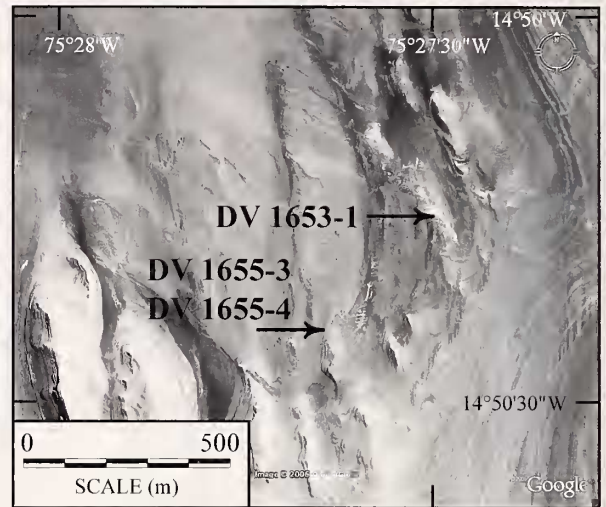


Figure 56. Type locality (DV 1655-4) of *Scalina isaacsoni*, sp. nov., 14 km north-northwest of Puerto Caballas, southern Peru.

*isaacsoni*, have weaker secondary spiral cords near both sutures or lack such spiral cords, and have axial costae that are more lamellar, recurved, and stand well above the spiral cords. *S. retifera* also has fewer (26 to 27) costae.

Specimens of *Scalina spathe* (Woodring, 1928) from the upper Pliocene Bowden Formation of Jamaica are also smaller than specimens of *S. isaacsoni* and have lamellar recurved costae like those on specimens of *S. retifera*. Specimens assigned to *S. weigandi* (Figure 45) by Woodring (1959) from the upper Miocene or lower Pliocene Chagres sandstone of Panama (Coates et al., 1992; Collins et al., 1996) are as large as specimens of *S. isaacsoni*, similarly sculptured, but have more pronounced and lamellate axial costae; they are morphologically intermediate between specimens of *S. isaacsoni* and the two Recent taxa, *S. deroyae* and *S. retifera*. Specimens of *S. edwilsoni* DuShane, 1977, from the lower to middle Pliocene Tirabuzón Formation of Baja California (Carreño, 1981) have a wider spire angle (about 21 to 22 degrees), lamellar extensions on many costae, and occasionally intercalated secondary spiral cords (e.g., spiral formulae wEDuCBAr and wEDCBAr; new photographs of the holotype and a paratype were provided by M. C. Perrilliat, 2006). Fragments of *Scalina* from the middle Pliocene Agueguexquite Formation of southern Mexico (*Scalina* aff. *S. pseudoderoyi*; see Perrilliat, 1972) may be assignable to *S. edwilsoni*.

Specimens of *Scalina isaacsoni* resemble those of the much shorter (<20 mm) and slightly broader (spire angle 19 to 21 degrees) late early Miocene Californian *S. whitei* (Keen, 1943; Addicott, 1970). The spiral formula of the Californian species is close to that of *S.*



*isaacsoni* (wEDCBarr or WEDCBarr) and for comparable sized whorls the number of costae is similar, but spiral cords of *S. whitei* are wider and secondary spiral cords 'r' are usually more numerous. Specimens of *S. isaacsoni* also resemble the single small specimen of *S. reticulata* Martin, 1904, from the middle Miocene Calvert Cliffs of Maryland (Martin, 1904; Andrews, 1988). The Maryland specimen has spiral cords that are less evenly spaced and intermediate in complexity between *S. isaacsoni* and the pair of late early Miocene species, *S. belti* and *S. kendacensis*.

**Material:** (all UWBM and MUSM INV specimens are middle Miocene syntypes from Peru) MUSM INV 150, DV 1655-4, L (29.5), W 15.2; MUSM INV 151, DV 1655-3, L 20.1, W 9.3; MUSM INV 152, DV 1655-3, L 16.1, W 5.4; MUSM INV 153, DV 1655-3, L 17.5, W 6.2; UWBM 98107, DV 1655-4, L (40.7), W (14.5); UWBM 98108, DV 1655-4, L (27.3), W 11.7; UWBM 98109, DV 1653-1, L 29.7, W 11.0; UWBM 98110, DV 1655-3, L 18.6, W 6.6; UWBM 98111, DV 1655-3, L 22.6, W 7.6. *Scalina* aff. *S. isaacsoni*: USNM 562641, USGS locality 16937, Panama, late Miocene to early Pliocene, L(26.8), W 14.0; USNM 562642, USGS 16937, L (20.4), W 14.6.

**Occurrence:** Early middle Miocene: southern Peru.

*Scalina belti*, sp. nov.

Figures 46–48

*Scalina pseudoleroyi* (Maury). Jung, 1965, p. 493, pl. 65, fig. 6.

**Diagnosis:** Spire angle 15 degrees. Interspaces between steeply rounded primary spiral cords with medial secondary spiral cord.

**Description:** Shell length to 30 mm. Spire angle 15 degrees. Whorls moderately convex, evenly rounded; sutures moderately impressed; shoulder poorly delimited. Protoconch unknown. Spire incomplete; teleoconch with at least six whorls; sculpture moderately reticulate, spiral elements stronger than axial elements. Axial sculpture of 43 evenly spaced thin costae. Costae rarely standing above spiral cords, not extended on shoulder or elsewhere. Spiral formulae wEDCBarr (early whorl) and wEvDuCtBsaRrr (body whorl). Primary spiral cords evenly spaced; 'B,' 'C,' 'D,' and 'E' equally strong. Interspaces between primary spiral cords with medial secondary spiral cord; broad interspace between 'E' and anterior suture. Spiral cords steeply rounded, elevated, half as wide as interspaces or narrower. Interspaces with reticulation of minute tertiary spiral and axial threads. Basal disk absent; basal region moderately inclined, planar, with 12 closely spaced secondary spiral cords, extensions of

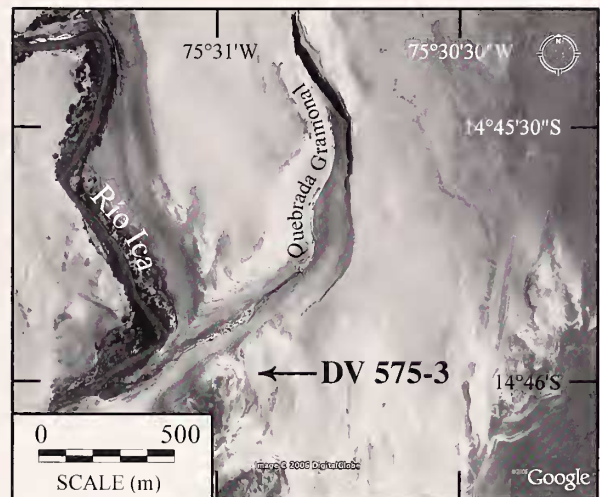


Figure 57. Type locality (DV 575-3) of *Scalina belti*, sp. nov., near juncture of Quebrada Gramonal and the Río Ica, southern Peru.

costae, and tertiary spiral axial threads; bounded by primary spiral cord. Aperture ovate, outer lip and most of columella missing. Umbilicus absent.

**Type Locality:** DV 575-3, south wall of Quebrada Gramonal near its juncture with the Río Ica, in cross-bedded delta foresets, Chilcatay Formation (Figure 57). Southern Peru, lower Miocene.

**Etymology:** Named for Edward S. Belt, the author's sedimentology and paleontology professor at Amherst College from 1975 to 1976.

**Discussion:** Peruvian specimens of the late early Miocene *Scalina belti* differ from those of early middle Miocene *S. isaacsoni* in several respects: they are narrower, they have more numerous but less elevated axial costae, and they have a medial secondary spiral cord between each pair of primary spiral cords. In these features they resemble specimens of *S. kendacensis* Jung, 1971, from the lower to middle Miocene Grand Bay, Belmont, and Carriacou Formations of Carriacou (Jung, 1971; Donovan et al., 2003), which also have medial secondary spiral cords, but the Peruvian specimens have less well developed costae that lack the shoulder extensions seen on the Carriacou species. In this latter respect, as in all others observed, the Peruvian specimens are identical to those from upper lower Miocene beds of the Cantaure Formation (Paraguana Peninsula, northwestern Venezuela) assigned to *S. pseudoleroyi* by Jung (1965). Specimens of *S. belti* differ from those of the slightly older *S. brophyi* of the Pisco Basin by having fewer secondary spiral cords near both sutures and secondary cords that are intercalated medially between much stronger primary spiral cords.

**Material:** UWBM 98100, DV 575-3, holotype, Peru, early Miocene, L (23.0), W 8.6; MUSM INV 147, DV 575-3, L (7.9), W 6.0; UWBM 98112, Chilcatay Hills, Peru, early Miocene, L (49.8), W (16.9).

**Occurrence:** Late early Miocene: northwestern Venezuela to southern Peru.

*Scalina brophyi*, sp. nov.

Figures 49–52

**Diagnosis:** Shell length to 50 mm. Spire angle 18 degrees. Secondary cords numerous near both sutures, one each between primary spiral cords.

**Description:** Shell length to 50 mm. Spire angle 18 degrees. Whorls moderately convex, evenly rounded; sutures moderately impressed. Protoconch unknown. Spire incomplete; teleoconch with at least nine whorls. Sculpture reticulate; spiral elements stronger. Axial sculpture of an estimated 50 evenly spaced thin costae, occasionally thickened; rarely lamellar. Costae stand slightly above spiral cords, sometimes extended at suture. Spiral formula wwEvDuCtBsArrrr or wwEvDuCtBsArrrrrr. Primary spiral cords evenly spaced, interspace between 'E' and anterior suture slightly broader; 'B,' 'C,' and 'D' strongest. Anterior primary spiral cords with anterior ramp; posterior spiral cords steeply rounded anteriorly and posteriorly, less than half the width of adjacent interspaces. Interspaces with non-medially situated secondary spiral cords, also with reticulation of minute tertiary spiral and axial threads. Basal disk absent; basal region steeply inclined, planar, with 20 secondary spiral cords, extensions of axial costae, and minute spiral and axial threads; bounded by strong spiral cord. Aperture ovate, poorly preserved. Umbilicus absent.

**Type Locality:** DV 478-3, Lomas Chilcatay, above orange sandstones of Chilcatay Formation on hillside south of Comotrana-Carhuas road, east of Bahia de la Independencia, southern Peru (Figure 58). Beds represent shoaling episode on outer shelf. Lower Miocene.

**Etymology:** Named for Gerald P. Brophy, the author's mineralogy professor at Amherst College in 1976.

**Discussion:** Specimens of *Scalina brophyi* differ from those of younger species in southern Peru by having a greater number of secondary spiral cords between the suture and primary spiral cord 'A,' and from those of all younger species from Peru other than *S. belti* by having intercalated secondary spiral cords between all primary spiral cords. Specimens of the slightly younger *S. belti* have fewer secondary spiral cords near both sutures and the secondary spiral cords are medially situated. Specimens of the Pliocene *S. pseudoleroyi* have

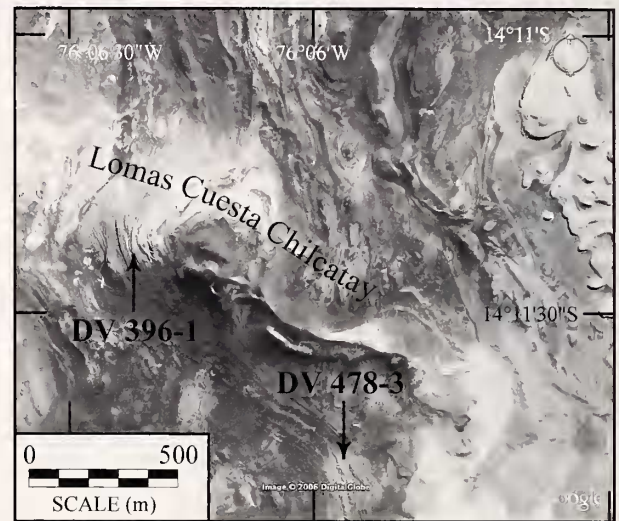


Figure 58. Type locality (DV 478-3) and second locality (DV 396-1) with *Scalina brophyi*, sp. nov., on southwest face of Lomas Cuesta Chilcatay, southern Peru.

wider spire angles and lack intercalated secondary spiral cords.

**Material:** UWBM 98101, DV 478-3, holotype, Peru, early Miocene, L 48.6, W 18.0; MUSM INV 148, DV 478-3, paratype, L (31.8), W 13.0; UWBM 98102, DV 478-3, paratype, L (13.1), W 9.9; UWBM 98103, DV 396-1, Peru, early Miocene, L (21.8), W 14.0.

**Occurrence:** Early Miocene: southern Peru.

*Scalina foosei*, sp. nov.

Figures 53–55

**Diagnosis:** Spire angle 15 degrees. Teleoconch with eight whorls. Sculpture of weakly rounded primary spiral cords and intervening secondary spiral cords. Basal disk present, not bounded by primary spiral cord.

**Description:** Shell length about 35 mm. Spire angle 15 degrees. Whorls weakly convex, evenly rounded; sutures weakly to moderately impressed. Protoconch less than two whorls; smooth. Teleoconch with eight whorls. Sculpture weakly reticulate; spiral elements stronger. Axial sculpture of about 75 costae, most regularly spaced, some standing above spiral cords; lamellar near sutures, worn elsewhere. Spiral formula wwwEvDuCtBsARr. Primary spiral cords broadly and symmetrically triangular or weakly rounded. Primary spiral cords unevenly spaced. Interspaces worn, but with hint of tertiary reticulation. Basal disk present, worn, but with trace of secondary spiral cords; not bounded by primary spiral cord. Aperture mostly



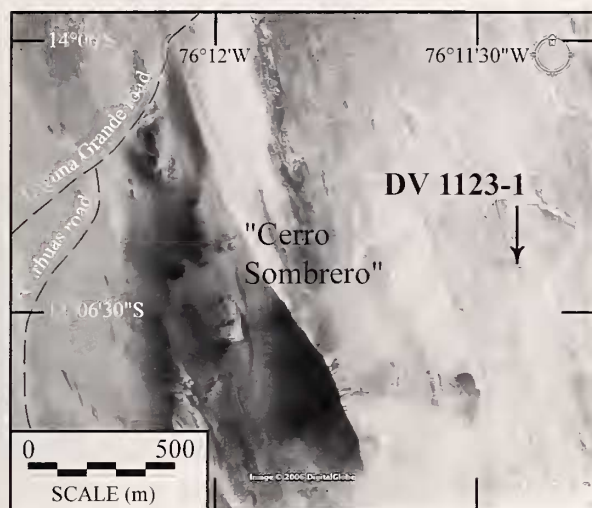


Figure 59. Type locality (DV 1123-1) of *Scalina foosei*, sp. nov., near the informally named Cerro Sombrero, between Laguna Grande and Pozo Santo, southern Peru.

destroyed: ovate, slightly spatulate at columella. Umbilicus absent.

**Type Locality:** DV 1123-1, southeast corner of informally named Cerro Sombrero in basal sandstones of the Otuma Formation, southern Peru (Figure 59). Late Eocene.

**Etymology:** Named in memory of Richard M. Foose, the author's professor of introductory geology, oceanography, and structural geology at Amherst College from 1973 to 1976.

**Discussion:** The sole specimen of *Scalina foosei* was compared with specimens of two Paleogene species of *Scalina* from the northeastern Pacific Ocean, *S. becki* (Durham, 1937) and *S. berthiaumei* (Durham, 1937), as well as figures of other taxa from Oregon and Washington [e.g., *S. aragoensis* (Durham, 1937), *S. dickersoni* (Durham, 1937), *S. lincolniensis* (Weaver, 1916); see Durham (1937), Weaver (1942), and Hickman (1969)], California [*S. pinolensis* (Clark, 1918); *S. atwoodi* (Dall, 1908), see Dall, 1908b], and Paleogene species from the Gulf Coast of the United States and Mexico [e.g., *S. escandoni* (Gardner, 1945); *S. trigintanaria* (Conrad, 1848) and related taxa (Gardner, 1945; MacNeil & Dockery, 1984); *S. menthafontis* MacNeil, 1984; *S. rubricollis* MacNeil, 1984; and *S. macula* Garvie, 1996]. Western American Paleogene species, including *S. foosei*, usually have retractive costae that merge tangentially with the posterior suture, a character not usually seen on specimens of Neogene species from the eastern Pacific or western Atlantic Ocean or Recent species from any ocean (Weil et al., 1999; but see DuShane's (1977) description of *S. edvilsoni*). Speci-

mens of *Scalina foosei* have well differentiated primary and secondary spiral cords not seen on specimens of other Paleogene species of *Scalina* from the Pacific Northwest or Gulf Coast of the U.S and Mexico, excepting *S. trigintanaria hopkinsi* MacNeil, 1984, a species from the lower Oligocene Mint Spring Formation of the southeastern United States (Pettway & Dunn, 1990).

**Material:** (all specimens from Peru, late Eocene): UWBm 98104, DV 1123-1, holotype, L 32.5, W 9.1; MUSM INV 149, DV 1220-1, L (12.7), W (7.8); UWBm 98105, DV 631-8, L (16.6), W 6.7.

**Occurrence:** Late Eocene: southern Peru.

## DISCUSSION

Not all identifications of *Scalina* stand up to close scrutiny. A specimen of *Scalina whitei* (Keen, 1943) from lower Miocene strata on King George Island, near Antarctica (Karczewski, 1987) is an incorrectly identified, poorly preserved mold with some surface sculpture intact. The Californian Paleogene *Acrilla* (*Ferminoscala*) *durhami* Zinsmeister, 1983, has prominent spiral nodes and therefore is not a member of *Scalina*; it should also not be confused with *Ferminoscala durhami* Keen, 1943, which is herein considered a junior synonym of *S. whitei*. Specimens of the Californian Pleistocene *Scalina effiae* (Willet, 1939), described and figured by DuShane (1979), have fine spiral scratches unlike any seen on other specimens of *Scalina*, obscure spiral cords beneath the surface shell layer, and little difference between spiral sculpture above and below a faint basal spiral cord.

The epitoniid, *Scala* (*Acrilla*) *pompholyx* Dall, 1890, known only from a single specimen (*vide* DuShane, 1974) collected off the Galapagos Islands at a water depth of 1485 m, differs in so many characters from the suite of Cenozoic *Scalina* species in the Americas that its assignment to the subgenus is doubtful.

### Paleogene comparisons

The late Eocene epitoniid from southern Peru, *Scalina foosei*, has costae that are retractive at the posterior suture like those on many Paleogene species from North America. Specimens of Paleogene species from California, Oregon and Washington, however, have numerous equally developed primary spiral cords with few if any secondary spiral cords, as do most Paleogene species from the Gulf Coast of Mexico and the United States. The differentiation of primary and secondary spiral cords on the specimen of *S. foosei* is more like that seen on lower Oligocene Gulf Coast specimens of *S. trigintanaria hopkinsi* and specimens of the early Miocene Peruvian species, *S. brophyi*. De-

ciding if this similarity reflects a close phylogenetic relationship between *S. foosei* and the latter two species awaits the discovery of more Paleogene material from Central and South America.

#### The 'brophyi' and nested 'isaacsoni' clades

The 'brophyi' clade includes all Neogene American species of *Scalina*. These species differ from most Paleogene species by having steeply rounded spiral cords and costae that are not retractive at the posterior suture and are distinguished from most modern non-American taxa by a pattern of spiral ornamentation (spiral formula wEvDuCtBsAr or some variant) together with secondary spiral cords, that, if present, are generally much smaller than the primary spiral cords. Nested within the 'brophyi' clade is an 'isaacsoni' clade, which is characterized by strong primary spiral cords, greatly reduced secondary spiral sculpture, and increasingly lamellar costae that may stand well above the spiral cords.

Specimens of the oldest Neogene American species, *Scalina brophyi*, collected from southern Peru in strata of 23 to 19 Ma (DeVries, 1998), have anterior ramping of some spiral cords and numerous secondary spiral cords. The 17-Ma Peruvian and Venezuelan species, *S. belti*, the nearly identical early to middle Miocene eastern Caribbean *S. kendacensis*, and the less elongate early to middle Miocene southern Californian *S. whitei* more closely resemble *S. retifera*; they have a single intercalated secondary spiral cords between the primary spiral cords and fewer secondary spiral cords adjacent to the anterior and posterior sutures.

The oldest species in the nested 'isaacsoni' clade and the youngest species of *Scalina* from southern Peru is the middle Miocene *S. isaacsoni* (about 14 to 13 Ma; DeVries, 1998). Specimens of this species exhibit a further tendency towards reduced secondary spiral sculpture. Specimens have two 'r' secondary spiral cords adjacent to the posterior suture, an 'w' secondary spiral cord near the anterior suture, and no intercalated secondary spiral cords.

Late Miocene and Pliocene species of the 'isaacsoni' clade include the early to middle Pliocene *Scalina edwilsoni* from Baja California, and in the Atlantic Ocean, the late Miocene to Pliocene *Scalina weigaudi* (*sensu* Woodring, 1959) from Panama and the late Pliocene *S. spathe* from Jamaica. The 'isaacsoni' clade culminates with two Recent geminate species, the Pacific *S. deroyae* and Atlantic *S. retifera*, both of which have minimal secondary spiral sculpture. Together, the two Recent species occupy the range formerly inhabited by late Neogene taxa, except that *S. retifera* also ranges to Brazil and West Africa (Weil et al., 1999), whereas *S. deroyae* presently ranges no farther south than Ecuador (DuShane, 1970, 1974).

#### The 'cheneyi' clade

The oldest evidence in southern Peru of a departure from the strongly reticulate sculpture of the early Miocene species of the 'brophyi' clade and the more widely distributed middle Miocene-to-Recent 'isaacsoni' clade is the appearance of *S. cheneyi* in upper Miocene beds in southern Peru (about 9 Ma; Muizon & DeVries, 1985; DeVries, 1998). Specimens of *S. cheneyi* have primary spiral cords that are broader and lower than those of species from either ancestral taxa or taxa of the sister 'isaacsoni' clade; costae are weaker, secondary spiral cords are less numerous, a true basal disk is present, and the spire angle is wider. The oldest late Miocene specimens of *S. cheneyi* are small; younger late Miocene and early Pliocene specimens are as large as those of any older Peruvian species.

#### The 'pseudoleroyi' clade

Even larger than specimens of *Scalina cheneyi* and with a wider spire angle, anteriorly ramped primary spiral cords, and prominent tertiary threads overrunning the primary spiral cords, are specimens of the 'pseudoleroyi' clade, which lies nested within the 'cheneyi' clade and appeared in early Pliocene Caribbean waters as *Scalina pseudoleroyi*. The most widely distributed of the 'pseudoleroyi' taxa is *S. ferminiana*, which lived during the late Pliocene in the Pacific [northern Peru (DeVries, 1986), Ecuador (Pilsbry & Olsson, 1941; DuShane, 1988)] and Atlantic Ocean [*S. weigandi* (Böse, 1910) (= *S. ferminiana*), eastern side of the Isthmus of Tehuantepec, Mexico], but today is restricted to the Pacific Ocean. The appearance of this species on both sides of Central America, as well as the presence of the similar *S. mitchelli* in the Gulf of Mexico, indicates that populations of the 'pseudoleroyi' clade had become established in both the Pacific and Atlantic Ocean before the closure of the Isthmus of Panama.

#### The 'brunneopicta' clade

Elongate epitoniids with broad, flattened spiral cords and partly formed basal disks appear in the late Miocene in Panama (Woodring, 1959) and Pliocene in Ecuador (Pilsbry & Olsson, 1941) and have persisted until the present in the tropical eastern Pacific Ocean as *Scalina brunneopicta*. The spiral sculpture on these specimens resembles that of the less elongate, more convexly formed specimens of the Peruvian late Miocene *S. cheneyi*.

#### Phylogenetic summary of Neogene *Scalina* in the Americas

A stratigraphy-based phylogeny of American taxa of *Scalina* is presented in Figure 60. Species are arranged



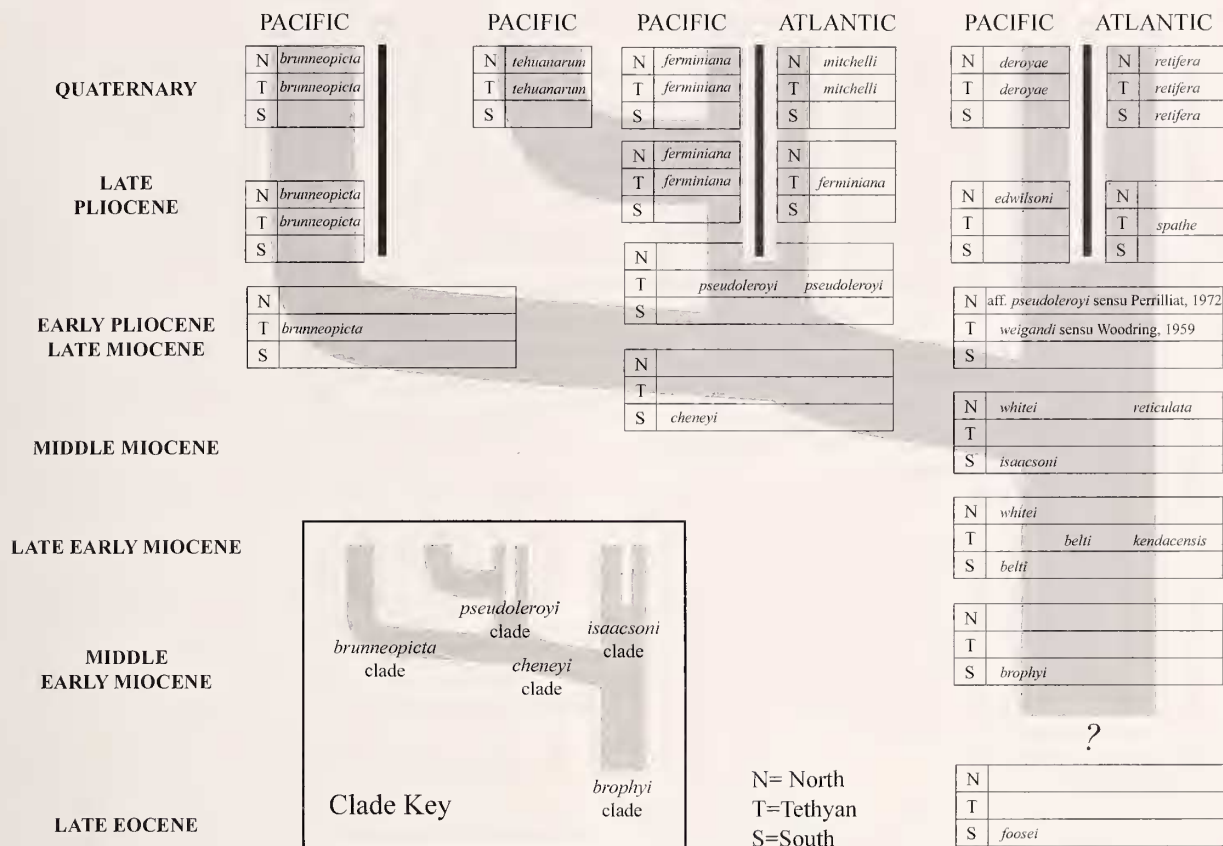


Figure 60. Proposed Neogene phylogeny of American species of *Scalina*. Species are placed according to age and geography (T = equatorial Tethyan realm; N = boreal tropical and subtropical latitudes; S = austral tropical and subtropical latitudes). Black vertical bars represent the separation of the Atlantic Ocean from the Pacific Ocean following the closure of the Isthmus of Panama. Clades of *Scalina* species are named at lower left.

according to their distribution north (N) and south (S) of a narrow Tethyan-equatorial region (T) and according to their geochronological range. No claim is made that one of the listed species is the direct ancestor or descendant of another so listed. Rather, the overlay of a phylogenetic tree on the Recent and fossil taxa shows a pattern of evolution, with the understanding that specific taxa may have evolved from a region or species in the Americas not yet represented in the figure.

Species of *Scalina* ranged from the Pacific Northwest of the United States to southern Peru and throughout the Gulf of Mexico during the Eocene and early to middle Oligocene. By the early Miocene, species of *Scalina* had disappeared from higher northern latitudes. Through much of the remainder of the Miocene, species of the 'isaacsoni' clade occupied American waters, albeit in lower latitudes by the late Miocene. During the late Miocene, a diversification within American *Scalina* yielded two new clades exemplified by the Recent *S. ferminiana* and *S. brunneopicta*. The evolutionary radiation, whose earliest manifestations

were *S. cheneyi* (Peru) and *Scalina* cf. *S. brunneopicta* (Panama), preceded the closure of the Isthmus of Panama by several million years (Coates et al., 1992).

In southern Peru, *Scalina* did not undergo the evolutionary radiation during the late Pliocene that was experienced by endemic taxa (DeVries, 2001). Rather, when sea-surface temperatures began to decline but before the Peruvian coast commenced a late Pliocene uplift, *Scalina cheneyi* disappeared from southern Peru, ending a 30 million year presence of *Scalina* in those austral waters. The local extinction of *Scalina* in southern Peru coincided with the local or complete extinction of other taxa with equatorial affinities in southern Peru (DeVries, 2001).

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## LITERATURE CITED

- ADAMS, H. & A. ADAMS. 1853–1858. The genera of recent Mollusca; arranged according to their organization. Volume 2. Van Voorst: London. 661 pp.
- ADDICOTT, W. O. 1970. Miocene gastropods and biostratigraphy of the Kern River area, California. United States Geological Survey Professional Paper 642:1–174.
- AKERS, W. H. 1981. Planktic foraminifera and calcareous nannoplankton biostratigraphy of the Neogene of Mexico. Addendum to Part I – Some additional mid-Pliocene localities and further discussion on the Agueguexquite and Concepción Superior beds. Tulane Studies in Geology and Paleontology 16(4):145–148.
- ALAMOV, V. & V. VALDIVIESO M. 1997. Lista sistemática de moluscos marinos del Perú. 2nd edition. Instituto del Mar del Perú, Callao; Peru. 183 pp.
- ALLMON, W. D. 1996. Systematics and evolution of Cenozoic American Turritellidae (Mollusca: Gastropoda) I: Paleocene and Eocene Coastal Plain species related to "*Turritella mortoni* Conrad" and "*Turritella humerosa* Conrad." Palaeontographica Americana 59:128.
- ANDREWS, G. W. 1988. A revised marine diatom zonation for Miocene strata of the southeastern United States. United States Geological Survey Professional Paper 1481:1–29.
- ARDOVINI, R. & T. COSSIGNANI. 2004. West African Seashells. L'Informatore Piceo: Ancona, Italy. 319 pp.
- BIANUCCI, G., G. CANTALAMESSA, W. LANDINI, L. RAGAINI & G. VALLERI. 1997. Paleontological and sedimentological observations on the Canoa Formation. Bollettino della Società Paleontologica 36(1, 2):85–96.
- BÖSE, E. & F. I. TOULA. 1910. Zur Jungtertiären Fauna von Tehuantepec. I. Stratigraphie, Beschreibung und Vergleich mit amerikanischen Tertiärfäunen. Jahrbuch der kaiserlichen und königlichen Geologische Reichsanstalt 60(2):215–276.
- CARREÑO, A. L. 1981. Ostrácodos y foraminíferos planctónicos de la loma del Tirabuzón, Santa Rosalía, Baja California Sur, e implicaciones bioestratigráficas y paleoecológicas. Universidad Nacional Autónoma de México, Instituto de Geología, Revista de Geología 5:55–64.
- CLARK, B. L. 1918. The San Lorenzo Series of Middle California. California University, Department of Geological Sciences Publications 11(2):45–234.
- CLENCH, W. J. & R. D. TURNER. 1950. The genera *Sthenorytis*, *Cirsotrema*, *Acirsa*, *Opalia* and *Ammaea* in the western Atlantic. Johnsonia 2(29):221–248.
- COATES, A. G., J. B. C. JACKSON, L. S. COLLINS, T. M. CRONIN, H. J. DOWSETT, L. M. BYBELL, P. JUNG & J. A. OBANDO. 1992. Closure of the Isthmus of Panama: the near-shore marine record of Costa Rica and western Panama. Geological Society of America Bulletin 104:814–828.
- COLLINS, L. S. 2006. New regional correlation of tropical Neogene sequences of coastal Ecuador. Geological Society of America, Abstracts with Programs 38(7):387.
- COLLINS, L. S., A. G. COATES, W. A. BERGGREN, M.-P. AUBRY & J. ZHANG. 1996. The late Miocene Panama isthmian strait. Geology 24:687–690.
- CONRAD, T. A. 1865. Catalogue of the Eocene and Oligocene Testacea of the United States. American Journal of Conchology 1(1):1–35.
- DALL, W. H. 1889. Reports on the results of dredgings, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78) and in the Caribbean Sea (1879–80), by the U.S. Coast Survey Steamer 'Blake,' Lieut.-Commander C. D. Sigsbee, U.S.N., and Commander J. R. Bartlett, U.S.N., commanding. XXIX. Report on the Mollusca. Part 2. Gastropoda and Scaphopoda. Bulletin of the Museum of Comparative Zoology at Harvard College 18:492.
- DALL, W. H. 1890. Scientific results of explorations by the U.S. Fish Commission Steamer Albatross, 7: Preliminary report on the collection of Mollusca and Brachiopoda obtained in 1887–88. Proceedings of the United States National Museum 12:219–362.
- DALL, W. H. 1896. On some new species of *Scala*. Nautilus 9: 111–112.
- DALL, W. H. 1908a. Reports on the dredging operations off the West coast of Central America to the Galapagos, to the West Coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U.S. Fish Commissioner steamer "Albatross," during 1891, Lieut. Commander Z. L. Tanner, U.S.N., Commanding. XXXVII. Reports on the scientific results of the expedition to the Eastern Tropical Pacific, in charge of Alexander Agassiz, by the U.S. Fish Commission steamer "Albatross," from October, 1904, to March, 1905, Lieut. Commander L. M. Garrett, U.S.N., Commanding. XIV. The Mollusca and the Brachiopoda. Bulletin of the Museum of Comparative Zoology at Harvard College 43(6):203–487.
- DALL, W. H. 1908b. Another large Miocene *Scala*. Nautilus 22(2):80–81.
- DEVRIES, T. J. 1986. The geology and paleontology of tablazos in northwest Peru. Doctoral dissertation, The Ohio State University, Columbus, Ohio. 964 pp.
- DEVRIES, T. J. 1988. The geology of marine terraces (tablazos) of northwest Peru. Journal of South American Earth Sciences 1(2):121–136.
- DEVRIES, T. J. 1998. Oligocene deposition and Cenozoic sequence boundaries in the Pisco Basin (Peru). Journal of South American Earth Sciences 11(3):217–231.
- DEVRIES, T. J. 2001. Contrasting patterns of Pliocene and Pleistocene extinctions of marine mollusks in western North and South America. Geological Society of America, Abstracts with Programs 33(3):A–35.
- DEVRIES, T. J. 2004. Eocene Mollusks from the Pisco Basin (southern Peru): Evidence for re-evaluating the age of the Otuma Formation. XII Congreso Peruano de Geología (Lima, Peru, October, 2004). Sociedad Geológica del Perú, Resúmenes Extendidos, Publicación Especial 6:436–439.
- DEVRIES, T. J. 2007. Cenozoic Turritellidae (Gastropoda) from southern Peru. Journal of Paleontology 81(2):331–351.



- DEVRIES, T. J., Y. NARVÁEZ, A. SANFILIPPO, N. MALUMIAN & P. TAPIA. 2006. New microfossil evidence for a late Eocene age of the Otuma Formation (southern Peru). XII Congreso Peruano de Geología (Lima, Peru, October, 2006). Sociedad Geológica del Perú, Resúmenes Extendidos, Publicación Especial.
- DEVRIES, T. J. & H. SCHRADER. 1997. Middle Miocene marine sediments in the Pisco Basin (Peru). Boletín de la Sociedad Geológica del Perú 87:1–13.
- DONOVAN, S., R. PICKERILL, R. PORTELL, T. JACKSON & D. HARPER. 2003. The Miocene palaeobathymetry and palaeoenvironments of Carriacou, the Grenadines, Lesser Antilles. *Lethaia* 36(3):255–272.
- DUNBAR, R. B., R. C. MARTY & P. A. BAKER. 1990. Cenozoic marine sedimentation in the Sechura and Pisco basins, Peru. *Palaeogeography, Palaeoclimatology, Palaeoecology* 77:235–261.
- DURHAM, J. W. 1937. Gastropods of the family Epitoniidae from the Mesozoic and Cenozoic rocks of the west coast of North America, including one new species by F. Earl Turner and one by Richard Allen Bramkamp. *Journal of Paleontology* 11(6):479–512.
- DUSHANE, H. 1970. Two new Epitoniidae from the Galapagos Islands. *The Veliger* 12(3):330–332.
- DUSHANE, H. 1974. The Panamic-Galapagan Epitoniidae. *The Veliger* 16(Supplement):1–84.
- DUSHANE, H. 1977. A new species of *Scalina* from the Pliocene of Baja California Sur, Mexico (Mollusca: Gastropoda). *Journal of Paleontology* 51(5):953–958.
- DUSHANE, H. 1979. The Family Epitoniidae (Mollusca: Gastropoda) in the northeastern Pacific. *The Veliger* 22(2):91–134.
- DUSHANE, H. 1988. Pliocene Epitoniidae of the Esmeraldas beds, northwestern Ecuador (Mollusca: Gastropoda). *Tulane Studies in Geology and Paleontology* 21(1):51–58.
- DUSHANE, H. & J. H. MCLEAN. 1968. Three new epitoniid gastropods from the Panamic Province. Los Angeles County Museum, Contributions in Science 145:1–6.
- GARDNER, J. 1945. Mollusca of the Tertiary formations of northeastern Mexico. Geological Society of America Memoir 11:332 pp.
- GARVIE, C. L. 1996. The molluscan macrofauna of the Reklaw formation, Marquez Member (Eocene: Lower Claibornian), in Texas. *Bulletins of American Paleontology* 111(352):177.
- GUPPY, R. J. L. 1867. On the Tertiary fossils of the West Indies with special reference to the classification of the Kainozoic of Trinidad. *Proceedings of the Scientific Association of Trinidad* 3:145–176.
- GUPPY, R. J. L. 1874. On the West Indian Tertiary fossils. *Geological Magazine (New Series)* 1:433–446.
- HICKMAN, C. S. 1969. The Oligocene marine molluscan fauna of the Eugene Formation in Oregon. University of Oregon, Museum of Natural History, Bulletin 16:112.
- JUNG, P. 1965. Miocene Mollusca from the Paraguaná Peninsula, Venezuela. *Bulletins of American Paleontology* 49(223):385–652.
- JUNG, P. 1971. Fossil mollusks from Carriacou, West Indies. *Bulletins of American Paleontology* 61(269):147–262.
- KARCZEWSKI, L. 1987. Gastropods from the Cape Melville Formation (Lower Miocene) of King George Island, West Antarctica. *Palaeontologia Polonica* 49:127–145.
- KEEN, A. M. 1943. New mollusks from the Round Mountain Silt (Temblor) Miocene of California. *Transactions of the San Diego Society of Natural History* 10(2):25–60.
- MACNEIL, F. S. & D. T. DOCKERY, III. 1984. Lower Oligocene Gastropoda, Scaphopoda, and Cephalopoda of the Vicksburg Group in Mississippi. *Mississippi Geological Survey Bulletin* 124:415 pp.
- MARTIN, G. C. 1904. Systematic paleontology. Miocene: Mollusca, Gastropoda. Maryland Geological Survey, Miocene volume, Pp. 131–270; Miocene, atlas, pls. 39–63.
- MAURY, C. J. 1925. A further contribution to the paleontology of Trinidad (Miocene horizons). *Bulletins of American Paleontology* 10(42):159–402.
- MELVILL, J. C. 1897. Description of thirty-four species of marine mollusks from the Arabian Sea, Persian Gulf, and Gulf of Oman. *Memoirs and Proceedings of the Manchester Literary and Philosophical Society* 41(3):25.
- MUIZON, C. DE & T. J. DEVRIES. 1985. Geology and paleontology of late Cenozoic marine deposits in the Sacaco area (Peru). *Geologische Rundschau* 74(3):547–563.
- NIELSEN, S. N., D. FRASSINETTI & K. BANDEL. 2004. Miocene Vetigastropoda and Neritimorpha (Mollusca: Gastropoda) of central Chile. *Journal of South American Earth Sciences* 17(1):73–88.
- OLSSON, A. A. 1942. Tertiary and Quaternary fossils from the Burica Peninsula of Panama and Costa Rica. *Bulletins of American Paleontology* 27(106):153–258.
- OLSSON, A. A. 1964. Neogene mollusks from northwestern Ecuador. Paleontological Research Institution: Ithaca, New York. 256 pp.
- PALMER, K. V. W. 1937. The Claibornian Scaphopoda, Gastropoda, and dibranchiate Cephalopoda of the southern United States. *Bulletins of American Paleontology* 7(32):730 pp.
- PEÑA, G. & G. M. 1976. Registros adicionales de gasterópodos marinos del Perú. *Anales Científicos (Universidad Nacional Agraria, Lima, Perú)* 14(1–4):1–8.
- PERRILLIAT, M. C. 1972. Monografía de los moluscos del Mioceno medio de Santa Rosa, Veracruz, México. Parte I. (Gasterópodos: Fissurellidae a Olividae). *Paleontología Mexicana* 32:130 pp.
- PERRILLIAT, M. C. 1992. Bivalvos y gasterópodos de la Formación Ferrotepec (Mioceno medio) de Michoacán. *Paleontología Mexicana* 60:49 pp.
- PETTWAY, W. C. & D. A. DUNN. 1990. Paleoenvironmental analysis of the lower Oligocene Mint Spring and Marianna Formations across Mississippi and southwestern Alabama. *AAPG Bulletin* 74:9.
- PHILIPPI, R. A. 1887. Fósiles Terciarios i cuaternarios de Chile. Brockhaus: Leipzig, Germany. 312 pp.
- PICKERILL, R. K., S. F. MITCHELL, S. K. DONOVAN & D. G. KEIGHLEY. 1998. Sedimentology and palaeoenvironment of the Pliocene Bowden Formation, southeast Jamaica. *Contributions to Tertiary and Quaternary Geology* 35:9–29.
- PILSBRY, H. A. & A. A. OLSSON. 1941. A Pliocene fauna from western Ecuador. *Proceedings of the Academy of Natural Sciences of Philadelphia* 93:1–79.
- PRINCZ, D. 1982. New records of living marine Gastropoda in Venezuela. *Veliger* 25(2):174–175.
- RÍOS, E. C. 1985. Seashells of Brazil. Empresas Ipiranga: Rio Grande, Brazil. 329 pp.
- SANCHEZ, F. 2003. Magnetic stratigraphy of the Miocene Round Mountain Silt and Olcese Sand, Bakersfield, California. *Geological Society of America, Abstracts with Program* 35(6):160.
- TAVERA, J. 1979. Estratigrafía y paleontología de la Forma-

- ción Navidad, Provincia de Colchagua, Chile (Lat. 30°50' S). Museo Nacional de Historia Natural (Santiago, Chile) Boletín 36:176.
- WEAVER, C. E. 1942. Paleontology of the marine Tertiary formations of Oregon and Washington. University of Washington Publications in Geology 5:789 pp.
- WEIL, A., L. BROWN & B. NEVILLE. 1999. The Wentletrap Book (Guide to the Recent Epitoniidae of the World). Evolver: Rome. 244 pp.
- WILLET, G. 1939. A new species of mollusk from the San Pedro Pleistocene. Bulletin of the Southern California Academy of Science 38(3):202–203.
- WOODRING, W. P. 1928. Miocene mollusks from Bowden, Jamaica. Part II. Gastropods and discussion of results. Carnegie Institute of Washington Publication 385:564 pp.
- WOODRING, W. P. 1959. Geology and paleontology of Canal Zone and adjoining parts of Panama. Description of Tertiary mollusks (Gastropods: Vermetidae to Thaididae). United States Geological Survey Professional Paper 306-B:147–239.
- ZINSMEISTER, W. J. 1983. New late Paleocene molluscs from the Simi Hills, Ventura County, California. Journal of Paleontology 57(6):1282–1303.

### Appendix Locality-Samples

ANSP 13640	Punta Blanca, Manabi Province, Ecuador. Pliocene.
ANSP 13641	Punta Blanca, Manabi Province, Ecuador. Pliocene.
DV 236-3	Three km south of the village of El Nuro, one km north of Cerro El Nuro, northern Peru. Cliff edge, Mancora Tablazo, lower part of section, on knoll below Mancora Tablazo surface, just below and north of gravel service road which proceeds from valley floor to tablazo surface; northwest corner of tablazo cliff face. [Description from 1981 (DeVries, 1986)]. Taime Formation, upper Pliocene.
DV 267-3	South face of Quebrada Carmen, three km south-southeast of El Alto, northern Peru. Taime Formation, upper Pliocene.
DV 396-1, 478-3	Lomas Chilcatay, southern Peru, orange sandstones between whitish tuffaceous fine sandstones. About 14°11'50"S, 76°06'00"W. Punta Grande 1:100,000 quadrangle. Chilcatay Formation, lower Miocene.
DV 523-2	Cerro Terrestrial, southern Peru, near top of section. 14°48'02"S, 75°23'02"W. Palpa 1:100,000 quadrangle. Pisco Formation, upper Miocene to lower Pliocene.
DV 523-4	Cerro Terrestrial, southern Peru, just below reddish beds in section. 14°48'02"S, 75°23'02"W. Palpa 1:100,000 quadrangle. Pisco Formation, upper Miocene to lower Pliocene.
DV 571-6	Alto Grande (El Jahuay of Muizon & DeVries, 1985), southern Peru. Near top of hill, west side of Panamerican Highway, shell beds across hillside. 15°26'57"S, 74°52'06"W. Acari 1:100,000 quadrangle. Pisco Formation, upper Miocene.
DV 575-3	Quebrada Gramonal, southern Peru; south wall, near juncture with the Río Ica. 14°45'40"S, 75°30'47"W. Lomitas 1:100,000 quadrangle. Chilcatay Formation, lower Miocene.
DV 599-2	Montemar, Sacaco Basin, southern Peru. Yauca 1:100,000 quadrangle. Pisco Formation, upper Miocene.
DV 631-8	Northwest of Loma Cuesta Chilcatay, southern Peru; continuous outcrop of sandstone below Chilcatay formation near Carhuas-Comotrana road. Fault slices with basement brought up on east side of main valley. 120.5 m in measured section. Punta Grande 1:100,000 quadrangle. Otuma Formation, upper Eocene.
DV 1123-1	Southeast corner of informally named Cerro Sombrero, basal yellow-white indurated sandstones on lower eastern side of small valley. 14°06'25"S, 76°11'08"W. GPS. Punta Grande 1:100,000 quadrangle. Otuma Formation, upper Eocene.
DV 1348-1	East side of Montemar, near Panamerican Highway. 15°31'18"S, 74°48'57"W. GPS. Yauca 1:100,000 quadrangle. Pisco Formation, late Miocene.
DV 1653-1	Nose of next to easternmost wind-carved north-south ridges east of the lowermost Río Ica and 'Labyrinth' zone; 'Sula' site of Stucchi fossil bird localities. Basal lagoonal sandstones. 14°50'16"S, 75°27'30"W. GPS. Lomitas 1:100,000 quadrangle. Pisco Formation, lower middle Miocene.
DV 1655-3	Southwest of 'Sula' site (DV 1653-1) by 400 m; shelly ridge in basal sandstones on west face of long ridge. 14 m above base of formation. 14°50'26"S, 75°27'38"W. GPS. Lomitas 1:100,000 quadrangle. Pisco Formation, lower middle Miocene.
DV 1655-4	Southwest of 'Sula' site (DV 1653-1) by 400 m; shelly ridge in basal sandstones on west face of long ridge. 16 m above base of formation. 14°50'26"S, 75°27'38"W. GPS. Lomitas 1:100,000 quadrangle. Pisco Formation, lower middle Miocene.
DeVries collection	<i>Scalina retifera</i> : Isla Escudo de Veraguas, Panama (Caribbean), dredged at 120 m water depth. Recent.
FMNH 145466	Yucatan, Mexico, off Campeche Banks, 40 m water depth. Recent.
FMNH 152778	Yucatan, Mexico, off Campeche Banks, 30 m water depth. Recent.
FMNH 00128594	Freeport, Texas. Recent.
LACM 1162	Gulf of Tehuantepec, Mexico, 59–68 m on mud bottom. 15°58'N, 95°00'W. Recent.
LACM 1236	(= AHF 147-34) Tagus Cove, Albermarle Island, Galapagos Islands, Ecuador, at 54 m water depth, on rock and coral. 0°16'38"S, 91°22'44"W. Recent.



Appendix  
Continued.

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LACM 127965	Guaymas, Sonora, Mexico, collected by shrimpers. Recent.
LACM 128144	Southeast of San Antonio Point, Guaymas, Sonora, Mexico, at 90 m water depth. Recent.
LACM 164927	Off Egmont Key, Pinellas County, Florida, at 121.9 m water depth. Recent.
LACM 38-8	Sihuantancjo, Guerrero, Mexico, at 36–73 m water depth. 17°38'N, 101°34'W. Recent.
LACM 55642	Southeast of San Antonio Point, Guaymas, Sonora, Mexico, at 90 m water depth. Recent.
LACMIP 11794	Onzole Formation, Esmeraldas Province, Ecuador. Pliocene.
PRI 4065	Charco Azul, Panama. Pliocene.
USGS 8410	Cuts on north (west) side of French Canal (East Diversion), Mount Hope, Canal Zone, Panama. Pliocene.
USGS 16937	Caribbean coast of Panama near mouth of Río Piña; road cut on west side of river about 90 m west of road fork. Massive fine-grained sandstone. Upper Miocene to lower Pliocene.
UCMP B1601	Coarse gravelly sand, east of hill 933. Caliente quadrangle, California. Upper part of Olcese Sand. Middle Miocene.
UCMP B1638	Caliente quadrangle, California. Lower part of Round Mountain Silt. Middle Miocene.
USGS 6064	North of Kern River, 11 miles southeast of Bakersfield, California. Lower part of Round Mountain Silt. Middle Miocene.
USGS M1608	South bank of Kern River. Rio Bravo Ranch quadrangle, California. Lower part of Round Mountain Silt. Middle Miocene.
USGS M1613	Rio Bravo Ranch quadrangle, California. Lower part of Round Mountain Silt. Middle Miocene.
USGS M2480	About 12 m stratigraphically above USGS M1613. Rio Bravo Ranch quadrangle, California. Lower part of Round Mountain Silt. Middle Miocene.

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